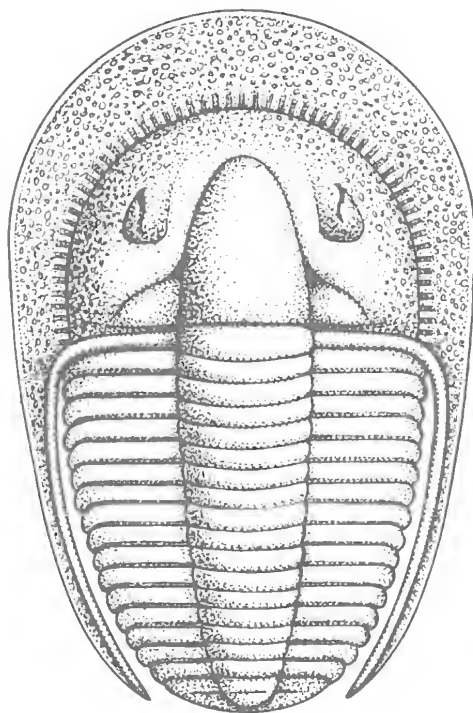


Records of the Western Australian Museum



Volume 21 Part 3 2002

Records of the Western Australian Museum

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Western Australian Museum

Francis Street, Perth, Western Australia 6000

Tel. (08) 9427 7000

Fax. (08) 9427 2882

E-mail ann.ousey@museum.wa.gov.au

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Printed and published by the Western Australian Museum

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ISSN 0312 3162

Cover: *Harpes perradiatus* Richter and Richter, 1943 from the early Devonian of Morocco.

Illustration by Jill Ruse

Cryptobarsac rubriops, a new genus and species of selizine Flatidae (Hemiptera: Fulgoromorpha) from grasstrees (*Xanthorrhoea preissii*) in south Western Australia

Murray J. Fletcher¹ and Melinda L. Moir²

¹Orange Agricultural Institute, NSW Agriculture, Forest Road, Orange, New South Wales 2800, Australia

²Dept of Environmental Biology, Curtin University of Technology, GPO Box U1987, Perth, Western Australia 6845, Australia

Abstract – *Cryptobarsac rubriops* gen. et sp. nov. (Hemiptera: Fulgoroidea: Flatidae) is described from grasstrees, *Xanthorrhoea preissii*, in southwestern Western Australia. The genus is placed in the Tribe Selizini. The taxonomy, zoogeography and plant associations of the Australian Selizini are discussed.

INTRODUCTION

The Australian Flatidae (Hemiptera: Fulgoromorpha) were reviewed by Fletcher (1988) who provided descriptions of 22 genera and a key for their separation. An electronic version of this key was published by Fletcher and Larivière (2001+). More than half of the genera are endemic and associated with the sclerophyllic flora that dominates most of the continent. Work by Medler (1986, 1990, 2000) has updated the generic identities of the Flatidae of Australia and neighbouring areas, particularly New Guinea, and these changes have been incorporated into Fletcher and Larivière (2001+).

Research by the second author has focussed on the hemipterous fauna of selected species of native sclerophyllic plants in regenerating bauxite mine pits and surrounding Jarrah (*Eucalyptus marginata* Smith) forest in SW Western Australia. Such intensively targeted collecting has found a number of species of unusual Hemiptera and one of these is described below as *Cryptobarsac rubriops* gen. et sp. nov. from *Xanthorrhoea preissii* Endl. (Xanthorrhoeaceae).

Abbreviations: ASCU, NSW Agricultural Scientific Collections Unit; WADA, Western Australian Department of Agriculture; WAM, Western Australian Museum.

Cryptobarsac gen. nov.

Type species: *Cryptobarsac rubriops* sp. nov.

Diagnosis

Habitus, from lateral aspect, as in Figure 1. Head short, with frons (Figure 2) broader than long, convex bearing median longitudinal carina and semicircular carina reaching to lower level of eyes

on each side and fused to percurrent apical marginal carina over median third. Vertex (Figure 3) very short, concave behind elevated anterior marginal carina. Pronotum (Figure 3) broadly rounded anteriorly, front margin reaching to anterior margin of eyes, carinate, extending laterally to almost meet hind margin, which is strongly and evenly concave. Dorsal pronotal surface flattish behind anterior curved carina, raised along median line on posterior half. Postocular prominences reduced in height but extended dorsoventrally. Mesonotum (Figure 3) broader than long, without median carina, lateral carinae well developed, posterior ends closer together than anterior. Tegmina (Figure 1) narrow, parallel-sided, evenly rounded posteriorly, angles not distinguished, outwardly prominent along basal portion of R. One subapical line present. Costal membrane as wide as costal cell then widening beyond apex of cell. R, M and Cu originating in basal cell, Rs separating some distance from base, Cu simple or branched before midlength. Hind tibia with two spines.

Etymology

The generic name, which is feminine, reflects the cryptic microhabitat in which the type species was found and the superficial similarity of the species to members of the genus *Barsac* Fletcher which occurs in drier habitats of Australia.

Notes

In the key provided by Fletcher (1988) this genus keys to couplet 4 on the basis of two hind tibial spines. It can be distinguished from *Mimophantia* Matsumura by having the head not extended in front of the eyes to form an extensive vertex and from *Anzora* by the presence of a clear percurrent

carina defining the anterior margin of the vertex and separating it from the frons. The key provided by Fletcher and Larivière (2001+) has been updated to include *Cryptobarsac*.

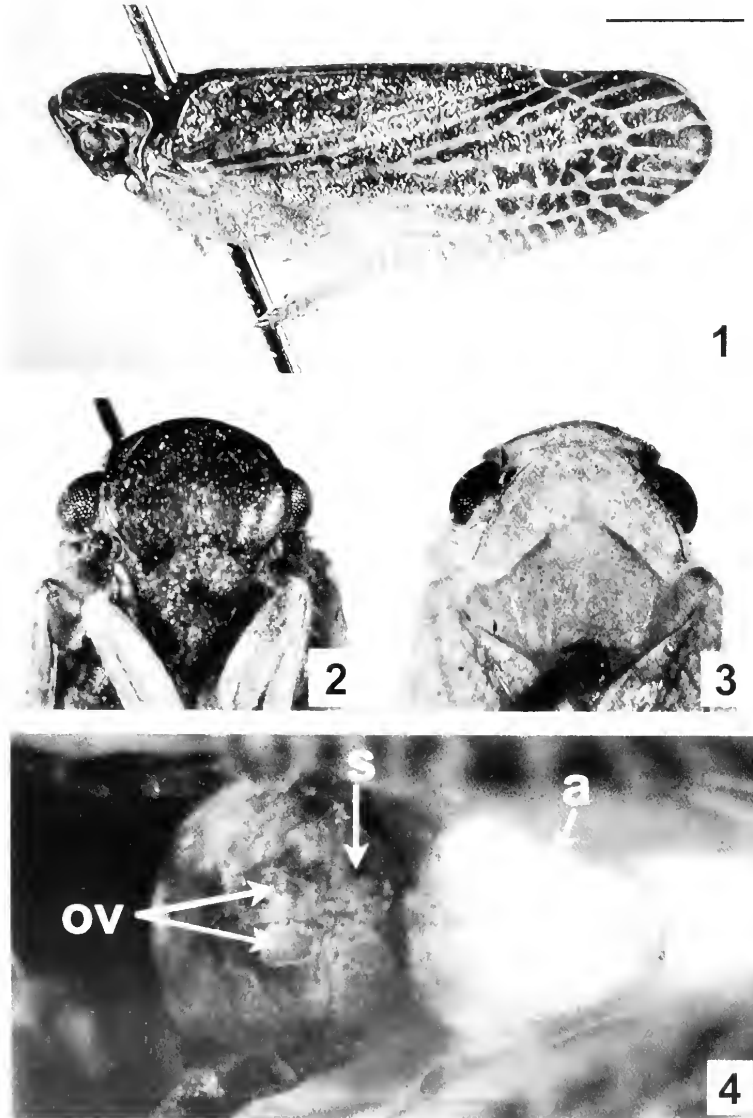
The short head, brown coloration and narrow parallel-sided tegmina outwardly prominent near the base of R (Medler, 1990, uses the term "bulla" for this feature) place *Cryptobarsac* in the tribe Selizini of the Subfamily Flatinae as defined by Melichar (1923).

Cryptobarsac rubriops sp. nov.
(Figures 1-6)

Types

Holotype

Male, Jarrahdale, SE of Perth, WA, beating *Xanthorrhoea preissii* in jarrah forest, 10 December 2000, M. Fletcher and M. Moir (WAM)



Figures 1-4 *Cryptobarsac rubriops* gen. et sp. nov.: 1, adult, habitus; 2, adult, facial view of head; 3, adult, dorsum; 4, female genitalia, ventral view, a: anal segment, s: secretory area, ov: ovipositor valves. Scale line: 1 mm

Paratypes

5 males, 5 females, Jarrahdale, WA 32°66'49"S 116°10'12"E, tree beating, *Xanthorrhoea preissii*, November 2001, Melinda Moir (2 males, 2 females: ASCU; 2 males, 2 females: WAM; 1 male, 1 female: WADA)

Description

Small, length (in midline from apex of head to tip of tegmen): males (n=6) 5.12 ± 0.22 mm, females (n=5) 5.47 ± 0.12 mm, brown, paler ventrally and on veins of tegmen, dark brown in cells. Some specimens pale brown on head and thorax with base of tegmen pallid. Eyes dark red in living specimens fading to dark reddish brown when dead. Male genitalia: pygofer (Figure 5) short, lacking process at posterodorsal corner which bears line of short setae. Subgenital plates (Figure 5) convex on basal half, apically truncate with well developed dorsal process straight and in line with apical truncation of plate. Anal segment long and broad with line of 3-4 short marginal setae slightly beyond midlength. Aedeagus as in Figure 6, with single pair of recurved processes on phallosoma. Female, with ovipositor valves reduced to paired ovate lobes. Posterodorsal section of pygofer flattened, bearing pad of dense packed setae, opposed to broadly expanded ninth (anal) segment held horizontally and at least 2/3 length of remainder of abdomen together (Figure 4).

Etymology

The specific name refers to the dark red eyes.

Notes

With other flatid genera, the male genitalia provide the most useful attributes for distinguishing between species. With only the single species known, it is presumed that the structure of the aedeagus (Figure 6) will provide diagnostic features of this species. The lack of a process on the posterodorsal corner of the pygofer and the presence of a strong process on the subgenital plates (Figure 5) may be generic features as also may be the strongly expanded anal segment of the female.

DISCUSSION

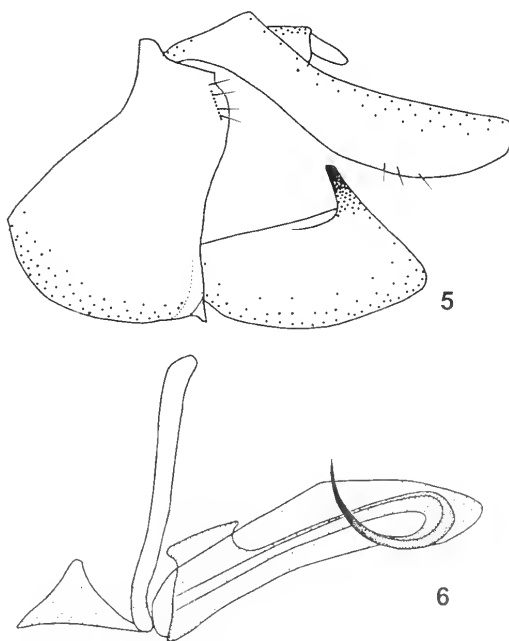
Taxonomy

Melichar (1923) provided keys to genera of the world Flatidae and included a number of Australian genera in the Tribe Selizini. These were *Massila* Walker, *Dascalina* Melichar, *Jamella* Kirkaldy and *Uxantis* Stål. Modifications to Melichar's (1923) generic arrangements were made by Metcalf (1957), who transferred *Uxantis* to the subfamily Flatoidinae, and Medler (1990), who transferred

Jamella, also to the Flatoidinae. New genera of Australian Selizini were added by Fletcher (1988) and, with the addition of the current new genus, the Australian Selizini now includes the five genera *Massila* with four species, *Dascalina* with four species, *Barsac* Fletcher with four species and the monotypic genera *Austrodascalina* Fletcher and *Cryptobarsac* gen. nov. All Australian Selizini are endemic at the generic level.

Of these genera, only *Barsac* and *Cryptobarsac* have a subapical line of crossveins. The general shape of the head and tegmina are similar between the species in the two genera as well. However, the four species of *Barsac* have similarities in the structures of the genitalia, which are quite different from the genitalia structures of *C. rubriops*. These include the subgenital plate being convex with outwardly curving dorsal process and the presence of two pairs of aedeagal processes one of which is mounted apically. In *C. rubriops* the subgenital plate is triangular with a straight dorsal process that does not curve outwards and the aedeagus has a single pair of non-apical processes.

In the key offered by Melichar (1923), *Cryptobarsac* keys to *Dascalina*, from which it differs in the shape of the tegmen, the apical margin being concave in *Dascalina*, and in the shape of the head, which is extended forward a short distance so that the frons curves ventrally to become almost horizontal in



Figures 5-6 *Cryptobarsac rubriops* gen. et. sp. nov.: 5, male terminalia, lateral view; 6, aedeagus, lateral view.

Dascalina. *Cryptobarsac* also differs from all other Australian Selizini in having two spines rather than one on the hind tibia. In Australia, only *Anzora unicolor* (Walker) (Tribe Nephesini, Subtribe Cryptoflatina) and *Mimophantia stictica* (Melichar), which was moved from the Tribe Phyllyphantini to the Tribe Phantiini by Medler (1988), have two spines on the hind tibia.

Biology

Fletcher (1979) provided details of the ovipositor and egg laying strategies of some species of Flatidae, many of which glue rafts of eggs onto leaf surfaces while others insert them into plant tissue. *Anzora unicolor* has a well developed sclerotised ovipositor bearing marginal teeth which is clearly capable of penetrating plant tissue while with other species the ovipositor is reduced to small lobes used for manipulating eggs into a surface raft. The Australian species of Selizini, including *C. rubriops*, have the reduced type of ovipositor consisting of small rounded lobes that would be incapable of cutting plant tissue. An expanded anal segment such as is found in *C. rubriops* (Figure 4) is also found in *Massila* and *Dascalina* and is presumably used either to help shape the egg mass or to spread a protective covering of wax over the eggs as was described in *Siphanta acuta* (Walker) by Muir and Kershaw (1912). Even in old pinned specimens, the anal segment usually still carries quantities of waxy filaments. These species presumably lay an egg mass similar to those laid by *Siphanta* species with the wax produced from the secretory area and manipulated by the large anal lobe. The degree of expansion of the anal segment found in female *C. rubriops* and species of *Massila* is greater than that found in species in other genera.

Habitat and plant associations

The Australian Selizini are frequently distributed in the more arid areas of the continent. *Barsac* species are found in inland areas of Western Australia, South Australia and Queensland. *Austrodascalina evansorum* Fletcher was described from Einasleigh River, a remote inland town in North Queensland, which has a monsoonal climate with extended periods of drought. *Dascalina* is distributed in similar monsoonal areas across northern Australia from Western Australia to Queensland. *Cryptobarsac* is described above from the northern Jarrah forest at Jarrahdale, 50km SE of Perth in Western Australia. This is an area of highly leached, nutrient deficient lateritic soils, with rainfall (1100 – 1300 mm per annum) confined mainly in the period from May to July (Ward *et al.* 1996). *Massila* species are distributed along the eastern coastal areas of Queensland with *M. sicca*

Walker extending into New South Wales as far south as Sydney.

Species of *Massila* are commonly found on exotic garden plants in coastal districts of eastern Australia but host associations are poorly known for most of the Australian Selizini. The only host records known prior to this current work is a paratype of *Barsac cocoa* Fletcher collected from foliage of *Eucalyptus gamophylla* F.Muell. (Myrtaceae) near Mt Bruce in the Pilbara district of Western Australia and the type series of *Austrodascalina evansorum* Fletcher collected from *Melaleuca* sp. (Myrtaceae) at Einasleigh River in North Queensland. *E. gamophylla* is a eucalypt species that grows as a mallee in deep sandy soils in arid regions of Western Australia, South Australia and the Northern Territory. *Melaleuca* is a genus of more than 200 species ranging from small shrubs to huge trees scattered across a wide range of habitats in Australia (Craven & Lepschi 1999). The most common species of the genus found in the Einasleigh River region of Queensland is *M. viridiflora* Gaertner (J.F. Donaldson, *pers. comm.* 2002).

The known specimens of *C. rubriops* were all collected by beating the "skirt" of dead leaves that normally adorn the upper parts of the trunk of *X. preissii*. The insects hide deep inside the skirt close to the main stem. Their narrow shape presumably helps them to move within the leaves of the grasstree where the dull brown coloration may provide further protection from detection. It is unknown whether they move out onto the living leaves to feed at night or whether they gain nourishment by feeding at the bases of the leaves under the skirt.

Mallee growth habits provide a microhabitat towards the base of the multiple trunks where bark and dead leaves accumulate providing protection for insects similar to that provided by the hanging skirt of dead leaves around the stem of *X. preissii*. However, any generalisation about microhabitats preferred by the species of Selizini found in Australia would be speculative without considerable further host data.

ACKNOWLEDGEMENTS

The authors acknowledge support from Alcoa World Alumina Australia and Curtin University of Technology for funding collection of specimens, Jonathan D. Majer and John M. Koch for their supervision of the second author and Karl E.C. Brennan and Erich S. Volschenk for informative discussions. We also thank John Donaldson, Queensland Dept of Primary Industries, Indooroopilly for the provision of habitat information on the type locality of *A. evansorum*.

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Redescription of *Lycidas chrysomelas* (Simon) (Araneae: Salticidae)

Julianne M. Waldock

Western Australian Museum, Francis Street, Perth,
Western Australia 6000, Australia

Abstract – *Lycidas chrysomelas*, previously known from only the holotype collected from Lion Mill, Western Australia, is found to be widespread in semi-arid Australia. The female is described for the first time, and the male is redescribed.

INTRODUCTION

In 1909 Eugene Simon described *Habrocestum chrysomelas* based on a single male that had been collected by Michaelsen and Hartmeyer on their expedition to south-western Australia in 1905. Subsequent published accounts have been limited to catalogue listings (Rainbow, 1911; Roewer, 1954; Bonnet, 1957) and a description of the male holotype and only known specimen by Žabka (1987). Recent collections of spiders from different regions of Australia have included many specimens of *L. chrysomelas*, which indicate that the spider has a widespread distribution in drier, semi-arid regions of the continent. I here present a redescription of the male based on recent material and the first description of the female of this little-known species.

MATERIALS AND METHODS

Material is lodged in the Western Australian Museum (WAM), South Australian Museum (SAM), Museum of Victoria (NMV), and Zoologisches Museum der Humboldt-Universität (ZMB). The names of some collectors have been abbreviated as follows in the *Material Examined* section: M.S. Harvey (MSH), J.M. Waldock (JMW), A.F. Longbottom (AFL), G. Friend (GF), D. Hirst (DH), P. Van Heurck (PVH), N.A. Guthrie (NG), B. Durrant (BD), L. King (LK), and material from the Salinity Action Plan Survey (SAP).

The female genitalia were examined by dissecting the epigynum from the abdomen and clearing it in 10% lactic acid for 10 minutes in a warm water bath. The epigynum was mounted in glycerol and drawn with a camera lucida fitted to an Olympus compound microscope. Other drawings were made using a graticule fitted to a Leica dissecting microscope.

SYSTEMATICS

Family Salticidae

Genus *Lycidas* Karsch

Lycidas Karsch, 1878: 25; Žabka, 1987: 451.

Jotus L. Koch, 1881: 1243. Synonymized by Žabka, 1987: 451.

Type species

of *Lycidas*: *Lycidas anomalus* Karsch, 1878: 26, by monotypy.

of *Jotus*: *Jotus auripes* L. Koch, 1881: 1243, by subsequent designation of Simon, 1901: 566.

Remarks

The male palpal structures indicate that the genera *Lycidas* and *Maratus* Karsch have a close affinity as Žabka (1987) has indicated. Features of the female genitalia and the general body configurations distinguish these salticids as separate genera. The presence of modified scutes and squamous hairs in males of both genera also indicate affinities, however the modifications of the scutes distinguish the genera. Males of *Maratus* have the abdominal scute developed into lateral flaps that fold under the abdomen, the scute is covered in squamous hairs of various colours and patterns. In species of *Lycidas* related to *L. chrysomelas* the males also have a scute with coloured squamous hairs but the scute is not developed into lateral flaps and there is a fringe of hairs along the edges. The tip of the embolus appears to be associated very closely with a conductor in *Lycidas* while in *Maratus* the conductor is more separated. The female genitalia of both *Lycidas* and *Maratus* are similar in that the spermatheca tend to be large but *L. chrysomelas* and related species have large, copulatory canals and

other structures such as proximal receivers are not evident. Proximal receivers are present in *Maratus* species.

Lycidas chrysomelas (Simon, 1909)

Figures 1–10

Habrocestum chrysomelas Simon, 1909: 201; Rainbow, 1911: 296; Roewer, 1954: 1119; Bonnet, 1957: 2064.

Lycidas chrysomelas (Simon): Žabka, 1987: 457, figures 19–22.

Material Examined

Holotype

♂, Lion Mill [= Mt Helena], Western Australia, Australia [31°53'S, 116°12'E], stat. 99, 22 May – 11 October 1905, W. Michaelsen, R. Hartmeyer (ZMB 18603).

Other Material

Australia: New South Wales: 2 ♂, Finlay [Finley], 35°39'S, 145°34'E, 16 February 1934, W.B. White (NMV). **South Australia:** 1 ♂, 1 km E. of Anamba East Dam, pitfall trap, 32°47'00"S, 140°15'30"E, 5–9 October 1992, N. P. W. S. South Olary Plain Survey (SAM N199578); 1 ♂, 2.5 km NW. of Bull Dam, pitfall, 32°31'30"S, 140°49'10"E, 28 September – 2 October 1992, N. P. W. S. South Olary Plain Survey (SAM N199579); 1 ♂, 2.5 km NNE. of Glenora, 33°27'30"S, 139°22'00"E, 23 October 1992, N. P. W. S. South Olary Plain Survey (SAM N199581); 1 ♂, Granite Downs [Station], near camp, 26°56'S, 133°30'E, December 1984, B. Guerin (SAM N1999501); 1 ♂, Hallett Cove, pitfall, 35°05'S, 138°30'E, 25 September 1994, A.J. McArthur (SAM N1997916); 1 ♂, 2 km W. of Hanging Knoll, pitfall, 26°19'23"S, 130°23'36"E, 4–8 May 1993, Pitjantjatjara Lands Survey, WW0601 (SAM N199589); 1 ♂, 1 ♀, Katarapko Game Reserve (= Murray River National Park), pitfall, 34°24'30"S, 140°34'10"E, 28 May 1991, A.J. McArthur (SAM N199583, N1995585); 1 ♂, 13 km N. of Keilira, 36°35'S, 140°10'E, 7 May 1975, DH (SAM N199593); 1 ♂, Kolay Hut, pitfall, 33°32'S, 135°36'E, 8–11 December 1989, DH (SAM N199587); 1 ♂, 17.5 km ENE. of Mt Cooperinna, pitfall, 26°19'20"S, 130°07'56"E, 6 May 1994, Pitjantjatjara Lands Biological Survey (SAM N199590); 1 ♂, 7.5 km NNW. of Mt Kintore, pitfall, 26°29'56"S, 130°27'22"E, 9 May 1994, Pitjantjatjara Lands Biological Survey, WA0401 (SAM N199591); 1 ♂, Muckera Rockhole, pitfall, 30°02'S, 130°03'E, September 1984, B. Guerin (SAM N1999496); 1 ♂, 1.4 km SE. of Mustering Dam, pitfall, 33°36'10"S, 139°37'40"E, 28 September – 31 October 1992, N. P. W. S. South Olary Plain Survey, KM0201 (SAM N199580); 1 ♂, Nangkita, burnt plot 6 Brawley's

Property, 35°22'S, 138°44'E, 30 January – 3 February 1998, S. Roberts (SAM N1999492); 1 ♂, 9 km SE. of Old Boolcoomata, pitfall, 32°10'36"S, 140°18'04"E, 26–31 August 1996, North Olary Plains Survey, OLA056 (SAM N1997914); 1 ♂, Poochera, Mudges Heritage site, pitfall, 32°43'S, 134°50'E, 29 October – 7 November 1995, A.J. McArthur, *Nothomyrmecia* Search (SAM N1997920); 1 ♂, same data except 7 November – 12 December 1995 (SAM N1997919); 1 ♂, 5 km S. of Quinyambie, pitfall, 30°15'28"S, 140°59'11"E, 1–6 October 1996, North Olary Plains Survey, CNE091 (SAM N1997915); 1 ♂, Salisbury North, [34°45'S, 138°37'E], 11 April 1982, DH (SAM N199592); 1 ♂, 4.4 km SE. of Sheep Camp Waterhole, pitfall, 29°45'41"S, 136°57'10"E, 30 September 1995, D.E.L.M. [Department for Environment and Land Management], STO4 (SAM N1997917); 1 ♂, Snodgrass Farm, 22.5 km SW. of Loxton, pitfalls, 34°33'S, 140°22'E, 28 May 1991, A.J. McArthur (SAM N199582); 1 ♂, 10.5 km SE. of Wares Peak, pitfall, 29°39'18"S, 135°46'00"E, 29 September – 5 October 1995, H.M. Owens, Painted Hills Survey (SAM N1997918); 1 ♂, 500 m SW. of Wataru, base of rock, WAT camp, 1.9 km WNW. of Mt Lindsay, ex grass, 27°01'41"S, 129°51'56"E, 16–19 October 1996, Pitjantjatjara Lands Survey (SAM N1999498); 1 ♂, 6 km WSW. of Womikata Bore Homeland, pitfall, 26°06'33"S, 132°05'57"E, 18–21 October 1994, J.A. Forrest, Pitjantjatjara Lands Survey (SAM N199588). **Victoria:** 1 ♂, 10 km E. of Edenhope, 36°59'S, 141°23'E, 20 September 1980, DH (SAM N199595). **Western Australia:** 2 ♀, Ajana Back Road [W. of Ajana], site NO 7, wet pitfall trap, 27°59'57"S, 114°37'55"E, 15 September 1998 – 30 March 1999, NG, CALM [Conservation and Land Management Dept] /SAP Survey (WAM T42244, T44819); 1 ♂, Amery–Benjabbering Road, near Amery (at turnoff to Minnivale), 31°09'S, 117°06'E, 20 May 1996, MSH (WAM 98/1604); 1 ♂, 2 ♀, Askew Road [S. of Mollerin Lake], site BE 6, wet pitfall trap, 30°35'46"S, 117°54'28"E, 15 September 1998 – 8 April and 25 October 1999, LK, CALM /SAP Survey (WAM T42242); 2 ♀, Bendering East Reserve Road, site KN 10, wet pitfall trap, 32°23'57"S, 118°23'12"E, 30 October – 19 May 1998, PVH, CALM/SAP Survey (WAM T41945); 1 ♀, Bendering Reserve Road, site KN 11, wet pitfall trap, 32°21'27"S, 118°29'46"E, 30 October 1997 – 19 May 1998, PVH, NG, CALM/SAP Survey (WAM T41946); 1 ♀, Boyup Brook – Arthur River, site DA 5, wet pitfall trap, 33°29'17"S, 116°53'12"E, 15 October 1999 – 1 November 2000, PVH *et al.*, CALM/SAP Survey (WAM T44820); 1 ♂, 1 ♀, Broom Gully, Di Russo Road, site HY 13, wet pitfall trap, 32°36'53"S, 119°06'10"E, 30 October 1997 – 19 May 1998, PVH, NG, CALM/SAP Survey (WAM T41931); 6 ♂, 1 ♀, Bruce Rock – Doodlakine Road, site KL 4, wet pitfall trap, 31°51'26"S, 118°06'14"E, 30 October 1997 – 22 May 1998, PVH, NG, CALM/

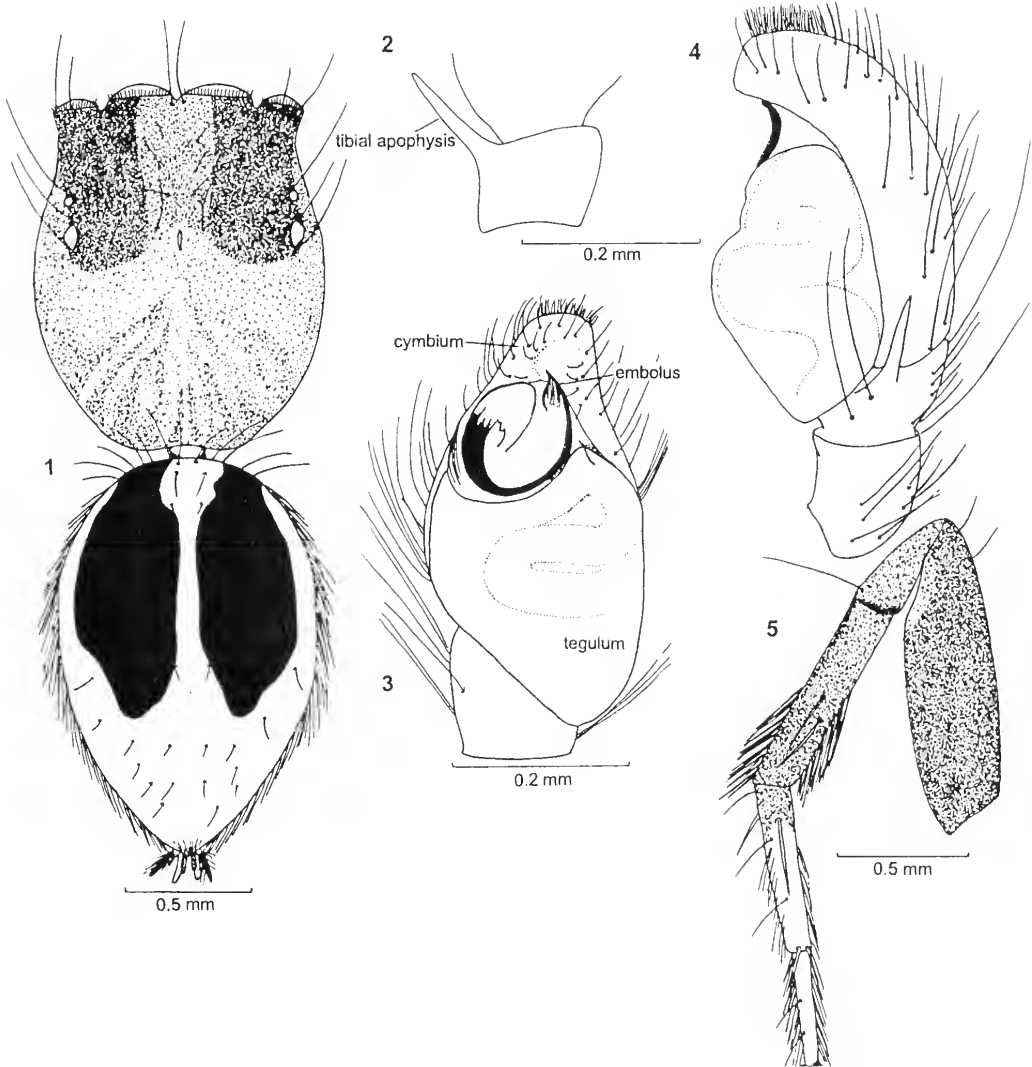
SAP Survey (WAM T41934 - 6); 2 ♂, same data except 22 May - 29 September 1998, NG (WAM T44821); 2 ♂, Bunce - King Road, NE. of Darkan, site DA 3, wet pitfall trap, 33°18'47"S, 116°48'22"E, 15 October 1999 - 1 November 2000, PVH *et al.*, CALM/SAP Survey (WAM T44822); 1 ♂, Buntine Nature Reserve, West, site WU 2, wet pitfall trap, 29°58'29"S, 116°34'59"E, 15 September 1998 - 7 April and 25 October 1999, LK, CALM/SAP Survey (WAM T42245); 1 ♂, Buntine Nature Reserve, North, site WU 3, wet pitfall trap, 29°58'16"S, 116°35'05"E, 15 September 1998 - 7 April and 25 October 1999, BD, CALM/SAP Survey (WAM T42246); 1 ♀, Buntine Nature Reserve, East, site WU 5, wet pitfall trap, 29°58'38"S, 116°34'27"E, 15 September 1998 - 25 October 1999, LK, CALM/SAP Survey (WAM T44823); 1 ♂, Burma Road [Nature] Reserve [29°00'S, 115°05'E], 18 September 1986, R.P. McMillan (WAM 99/208); 1 ♂, Burracoppin Nature Reserve, Powerline, site MN 3, wet pitfall trap, 31°24'39"S, 118°30'33"E, 30 October 1997 - 21 May 1998, PVH, NG, CALM/SAP Survey (WAM T41947); 2 ♂, same data except 21 May - 22 September 1998, NG (WAM T44824); 1 ♂, 5 ♀, Comitun Dam Nature Reserve, North, site KL 5, wet pitfall trap, 31°45'38"S, 118°03'47"E, 30 October 1997 - 22 May 1998, PVH, NG, CALM/SAP Survey (WAM T41937 - 40); 1 ♂, Commonwealth Road, West, [SE. of Kulin], site KN 3, wet pitfall trap, 32°44'13"S, 118°16'16"E, 30 October 1997 - 15 May 1998, BD, CALM/SAP Survey (WAM T42247); 1 ♂, Condungup, Daniell Road, 33°45'S, 122°32'E, 19 Jan. 1999, AFL (WAM T40623); 1 ♂, Cookinbin Nature Reserve, site MN 8, wet pitfall trap, 31°00'05"S, 118°14'00"E, 30 October - 15 December 1997, PVH, CALM/SAP Survey (WAM T41949); 3 ♂, Corackerup Nature Reserve, site 01, pitfall trap, 34°12'12"S, 118°42'00"E, October 1996, A. Sanders (WAM 98/1605-7); 2 ♂, Coyrecup Lake Nature Reserve, West, site DU 7, wet pitfall trap, 33°43'07"S, 117°51'18"E, 15 October 1999 - 1 November 2000, PVH *et al.*, CALM/SAP Survey (WAM T44825); 1 ♀, Cunderdin Road, North, NE. of Mukinbudin, site BE 4, wet pitfall trap, 30°38'03"S, 118°29'03"E, 15 September 1998 - 9 April and 25 October 1999, LK, CALM/SAP Survey (WAM T42248); 1 ♀, Darlington [31°54'S, 116°05'E], 1975-1979, G. H. Lowe (WAM T40624); 1 ♂, Dryandra Forest, Attunga Road, Skeleton Block, site NR 3, wet pitfall trap, 32°46'58"S, 116°51'54"E, 30 October 1997 - 14 May 1998, NG, CALM/SAP Survey (WAM T42249); 1 ♂, 1 ♀, Dryandra [Forest], Patonga Road, Smith Block, site NR 4, wet pitfall trap, 32°48'39"S, 116°53'23"E, 30 October 1997 - 14 May 1998, E. Ladhams, CALM/SAP Survey (WAM T41953); 2 ♂, same data except 14 May - 16 September 1998, LK (WAM T44837); 1 ♂, Drysdale River Station, in scrub, 15°42'S, 126°23'E, 30 May 1993, AFL (S. 1225) (WAM 98/1608); 1 ♂, Drysdale River Station, Woodhouse River Crossing area, [c. 15°42'S, 126°22'E], 5 August 1993, AFL (S. 1320) (WAM 98/1609); 1 ♂, Drysdale River Station, in truck, 15°42'S, 126°23'E, 10 December 1993, AFL (S. 1454) (WAM 98/1610); 2 ♀, 2 juveniles, Durokoppin [Nature] Reserve, sites H1, H2, wet pitfalls, 31°30'S, 117°44'E, 13-23 March 1992, GF (WAM 98/2125-8); 2 ♂, same data except sites H3, J1, 3-13 November 1992 (WAM 98/1611, T40625); 3 ♀, Durokoppin Nature Reserve, North, site KL 8, wet pitfall trap, 31°24'09"S, 117°45'32"E, 30 October 1997 - 22 May 1998, PVH, NG, CALM/SAP Survey (WAM T41941 - 2); 1 ♂, Durokoppin Nature Reserve, South, site KL 10, wet pitfall trap, 31°24'46"S, 117°45'16"E, 30 October 1997 - 22 May 1998, PVH, NG, CALM/SAP Survey (WAM T41943); 1 ♂, 1 ♀, East Yorkrakine [Nature] Reserve, sites K4, J2, [31°28'S, 117°41'E], 3-14 November 1988, D. Mitchell *et al.* (WAM 98/1612, T42051); 4 ♂, same data except sites J2, J4, K3, 19-29 May 1989, GF (WAM 98/1613-6); 1 ♂, same data except site K1, 3-13 November 1989 (WAM 98/1617); 1 ♂, same data except site J4, 17-27 November 1989 (WAM T44323); 1 ♂, same data except site K3, 18-28 March? 1990 (WAM T44322); 2 ♂, Elashgin Nature Reserve, granite site, wet pitfall trap, 31°20'07"S, 117°26'10"E, 7 September - 29 November 1999, JMW, I.Studley (WAM T40633); 1 ♂, Eneabba, R.G.C. Mineral Sands, site 1, pitfall trap, 29°56'S, 115°17'E, 30 October 1997, R.P. McMillan (WAM 98/1941); 1 ♂, same data except site 3, 31 October 1997 (WAM T40626); 1 ♀, Erikin Road, site KL 2, wet pitfall trap, 31°57'51"S, 117°56'05"E, 30 October 1997 - 22 May 1998, PVH, NG, CALM/SAP Survey (WAM T41932); 2 ♂, Gidgegannup, Waterford Road, [31°48'S, 116°11'E], 12 January 1992, JMW (WAM 98/1618-9); 1 ♂, Glen Helen Gorge, 25°00'S, 128°09'E, 14 January 1990, MSH, T.F. Houston (WAM 98/1620); 1 ♂, 1 ♀, Gura Road, East, [N. of Congelin], site NR 9, wet pitfall trap, 32°46'09"S, 116°57'08"E, 30 October 1997 - 12 May 1998, NG, CALM/SAP Survey (WAM T42250); 1 ♂, Heitmans Scrub, site M4, pitfalls, 31°31'S, 117°37'E, 16-26 March 1989, GF *et al.* (WAM 98/1621); 1 ♂, same data except 3-13 November 1992 (WAM 98/1622); 1 ♂, Hotham River National Park, site NR 1, wet pitfall trap, 32°36'40"S, 117°06'00"E, 15 May - 16 September 1998, PVH, CALM/SAP Survey (WAM T44826); 2 ♀, Howatharra Nature Reserve, site NO 3, wet pitfall trap, 28°32'45"S, 114°39'56"E, 15 September 1998 - 18 October 1999, NG, CALM/SAP Survey (WAM T42251); 1 ♂, 20 km E. of Hyden, [c. 32°25'S, 119°02'E], August 1990, D. Knowles (WAM 98/1623); 1 ♂, NE. of Jarrahdale, Alcoa minesite, site 1 (NE. of Johnson/Chandler Rds Junction), [c. 32°17'S, 116°06'E], 1986, P.R. Mawson (WAM T44708); 1 ♂, Jilakin Lake, site KN 1, wet pitfall trap, 32°40'29"S, 118°20'10"E, 30 October 1997 - 15 May 1998, PVH, NG, CALM/

SAP Survey (WAM T41944); 1 ♂, same data except Lk (WAM T42252); 1 ♂, Jingemina Hill, Watheroo National Park, site DN 2, wet pitfall trap, 30°15'21"S, 116°01'17"E, 15 October 1999 – 1 November 2000, PVH *et al.*, CALM/SAP Survey (WAM T44827); 3 ♀, Jouerdine Nature Reserve, site BE 3, wet pitfall trap, 30°38'11"S, 118°25'39"E, 15 September 1998 – 9 April and 25 October 1999, LK, CALM/SAP Survey (WAM T42253, T44828); 2 ♀, Julimar Conservation Park, NE., site JB 8, wet pitfall trap, 31°23'59"S, 116°19'06"E, 15 September 1998 – 22 April and 4 November 1999, BD, CALM/SAP Survey (WAM T44829); 1 ♂, Julimar Conservation Park, North, site JB 12, wet pitfall trap, 31°24'06"S, 116°09'49"E, 15 September 1998 – 4 November 1999, NG, CALM/SAP Survey (WAM T44830); 3 ♂, same data except site JB 13, 31°21'21"S, 116°13'04"E, BD (WAM T42254); 2 ♀, SE. of Kadjji Kadjji, North along powerline, site MO 8, wet pitfall trap, 29°10'18"S, 116°23'16"E, 15 September 1998 – 1 April 1999, BD, CALM/SAP Survey (WAM T42255); 1 ♂, Karlgarin National Park, Hyden Road, site KN 5, wet pitfall trap, 32°29'59"S, 118°33'05"E, 15 October 1997 – 19 May 1998, PVH, CALM/SAP Survey (WAM T42256); 1 ♂, 1 ♀, Kellerberrin, 31°38'S, 117°43'E, no date, G.T. Smith (WAM 98/1525-6); 1 ♀, Koorda Road, nature reserve #22363, site WH 6, wet pitfall trap, 30°45'25"S, 117°05'26"E, 15 September 1998 – 29 April and 25 October 1999, BD, CALM/SAP Survey (WAM T44831); 1 ♂, Kulunilup Nature Reserve, East, site UN 8, wet pitfall trap, 34°20'00"S, 116°48'03"E, 15 October 1999 – 1 November 2000, NG, CALM/SAP Survey (WAM T44832); 1 ♀, Lake Campion Nature Reserve, site MN 12, wet pitfall trap, 31°10'09"S, 118°26'20"E, 30 October 1997 – 26 April 1998, E. Ladhams, CALM/SAP Survey (WAM T41952); 2 ♂, 1 ♀, Lake Fox, site HY 9, wet pitfall trap, 32°54'50"S, 119°28'32"E, 30 October 1997 – 20 May 1998, PVH, CALM/SAP Survey (WAM T41930); 2 ♂, same data except 20 May – 29 August 1998 (WAM T42257); 1 ♂, 3 ♀, Lake Gulson, site HY 8, wet pitfall trap, 32°47'11"S, 119°22'07"E, 30 October 1997 – 20 May 1998, E. Ladhams, CALM/SAP Survey (WAM T41929); 1 ♂, 1 ♀, Lily McCarthy Rock, site HY 10, wet pitfall trap, 32°41'35"S, 119°20'25"E, 30 October 1997 – 20 May 1998, E. Ladhams, CALM/SAP Survey (WAM T42259); 2 ♀, Lochada Road Nature Reserve, West, site MO 9, wet pitfall trap, 29°15'13"S, 116°22'05"E, 15 September 1998 – 1 April 1999, LK, CALM/SAP Survey (WAM T44834); 1 ♂, Mackie Creek Reserve, East, site YO 1, wet pitfall trap, 31°59'33"S, 117°01'19"E, 20 May – 5 November 1998, BD, CALM/SAP Survey (WAM T44835); 1 ♂, Manmanning Dam Nature Reserve, SE., site WH 8, wet pitfall trap, 30°54'53"S, 117°05'41"E, 15 September 1998 – 25 and 28 October 1999, LK, CALM/SAP Survey (WAM T42260); 1 ♀, Manmanning Dam Nature Reserve, site WH 7, wet

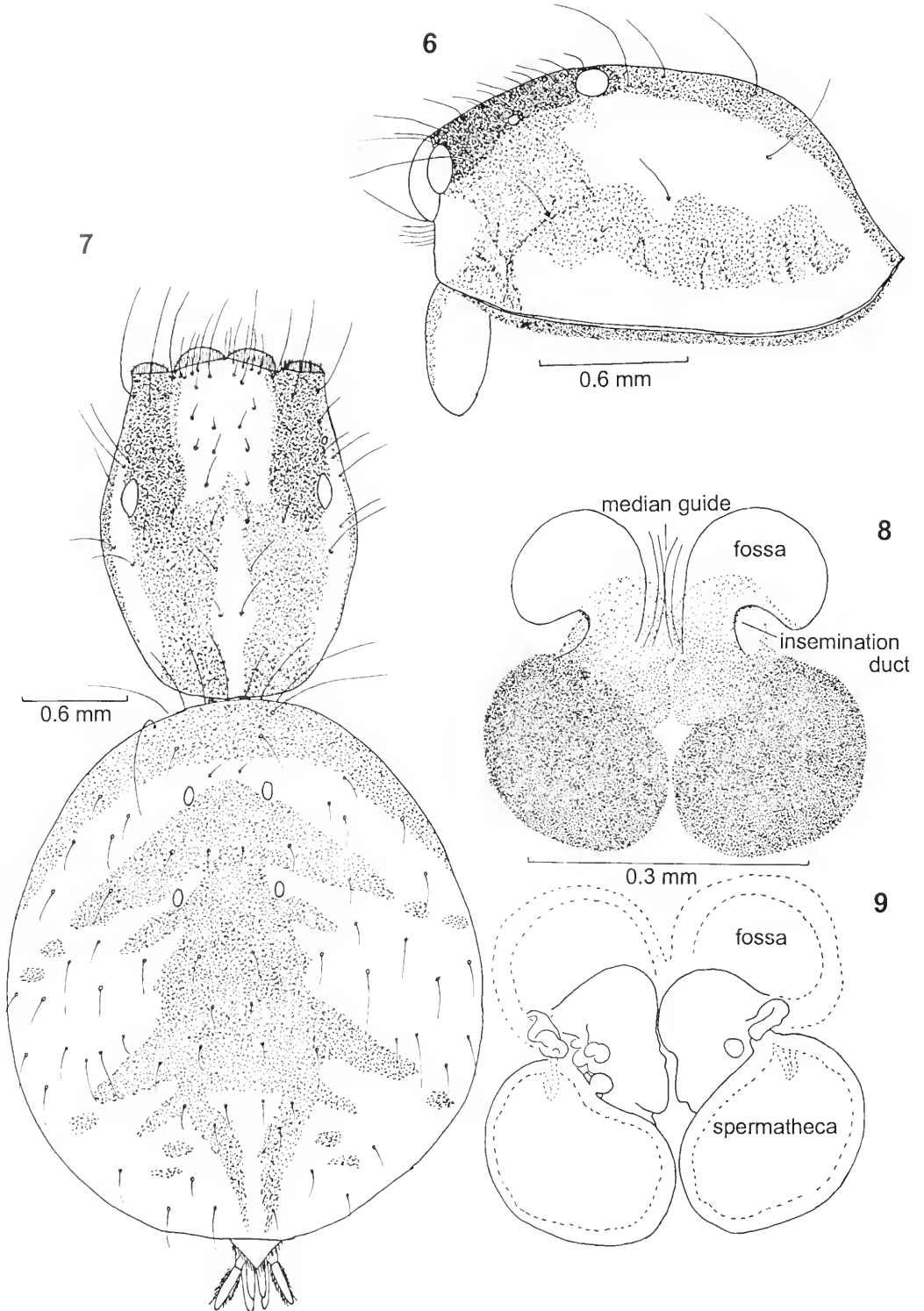
pitfall trap, 30°49'13"S, 117°04'58"E, 15 September 1998 – 29 April and 25 October 1999, LK, CALM/SAP Survey (WAM T42261); 1 ♀, Mollerin Lake, South, site BE 8, wet pitfall trap, 30°31'47"S, 117°34'45"E, 15 September 1998 – 25 October 1999, LK, CALM/SAP Survey (WAM T44833); 1 ♀, Mollerin Lake, West, site BE 10, wet pitfall trap, 30°31'41"S, 117°33'54"E, 15 September 1998 – 8 April and 25 October 1999, PVH, CALM/SAP Survey (WAM T42258); 2 ♂, [S. of Mollerin Lake], Rock, Long Muir Road, West, site BE 7, wet pitfall trap, 30°32'50"S, 117°33'56"E, 16 September 1998 – 8 April and 25 October 1999, PVH, CALM/SAP Survey (WAM T42243); 4 ♂, 3 ♀, Moonijin Nature Reserve, site WH 11, wet pitfall trap, 30°54'57"S, 117°09'05"E, 15 September 1998 – 25 October 1999, BD, CALM/SAP (WAM T42262, T 44836); 2 ♀, Mount Moore Nature Reserve, site MN 7, wet pitfall trap, 31°12'45"S, 118°18'15"E, 30 October – 15 December 1997, PVH, CALM/SAP Survey (WAM T41948); 2 ♂, 1 ♀, same data except 15 October 1997 – 21 May 1998 (WAM T42264); 1 ♀, Mount Stirling Road, site QU 10, wet pitfall trap, 31°59'27"S, 117°24'19"E, 30 October 1997 – 27 May 1998, PVH, NG, CALM/SAP Survey (WAM T41954); 3 ♂, 5 ♀, Noorajin Soak Nature Reserve, site WH 13, wet pitfall trap, 30°45'17"S, 117°14'30"E, 15 September 1998 – 18 October 1999, NG, CALM/SAP Survey (WAM T42263); 2 ♂, Packsaddle Plain via Kununurra, 15°49'S, 128°43'E, 26 October 1999, A. Postle (WAM T41824); 1 ♀, Parmelia, 15 Sicklemore Road, 32°15'S, 115°49'E, 25 December 1999, A.E. de Jong (WAM T42160); 1 ♂, Quairading Railway Water Supply, West, site QU 11, wet pitfall trap, 32°01'32"S, 117°21'58"E, 20 May – 5 October 1998, BD, CALM/SAP Survey (WAM T44838); 1 ♂, 1 ♀, same data except 30 October – 27 May 1998, E. Ladhams (WAM T42265); 1 ♀, same data except West, site QU 12, 32°01'15"S, 117°22'57"E, PVH, NG (WAM T41956); 1 ♂, 1 ♀, St Ronans Nature Reserve, North, site YO 12, wet pitfall trap, 31°52'30"S, 116°36'10"E, 30 October 1997 – 26 May 1998, E. Ladhams, CALM/SAP Survey (WAM T42266); 2 ♀, Salt River, Beverley Road, site QU 8, wet pitfall trap, 32°05'02"S, 117°23'33"E, 30 October 1997 – 26 May 1998, PVH, NG, CALM/SAP Survey (WAM T41955); 1 ♂, Sandplains Nature Reserve, West, site MN 4, wet pitfall trap, 31°35'48"S, 118°45'24"E, 28 April – 22 September 1998, NG, CALM/SAP Survey (WAM T44839); 1 ♂, 1 ♀, Snake Gully Nature Reserve, site WU 11, wet pitfall trap, 30°13'05"S, 116°56'36"E, 15 September 1998 – 7 April 1999, NG, CALM/SAP Survey (WAM T42267); 1 ♂, Talgomine Reserve, North, site MN 10, wet pitfall trap, 31°14'40"S, 118°24'25"E, 30 October – 15 December 1997, PVH, CALM/SAP Survey (WAM T41950); 1 ♀, same data except 10 October 1997 – 28 April 1998, PVH, NG (WAM T41951); 1 ♂, Tutanning Nature Reserve, East, site WK 8, wet

pitfall trap, 32°32'29"S, 117°16'50"E, 15 October 1997 – 11 May 1998, PVH, CALM/SAP Survey (WAM T42268); 4 ♀, 2 juvs, Uwara Nature Reserve, North, site ML 7, wet pitfall trap, 28°24'02"S, 115°34'34"E, 15 September 1998 – 1 April and 18 October 1999, BD, CALM/SAP Survey (WAM T44840); 1 ♂, 1 ♀, Walkaway Nature Reserve, site WH 12, wet pitfall trap, 30°48'08"S, 117°19'19"E, 15 September 1998 – 25 October 1999, BD, CALM/SAP Survey (WAM T44841); 1 ♂, 1 ♀, Wansbrough Nature Reserve, North, site ST 11, wet pitfall trap, 34°09'08"S, 117°40'09"E, 18 October 1999 – 30 May 2000, NG, CALM/SAP Survey (WAM T44842); 1 ♂, private property E. of Watheroo National Park, site DN 4,

wet pitfall trap, 30°09'17"S, 115°57'38"E, 15 October 1999 – 1 November 2000, PVH *et al.*, CALM/SAP Survey (WAM T44843); 2 ♂, Yarding Nature Reserve, site KL 3, wet pitfall trap, 31°55'02"S, 117°58'49"E, 30 October 1997 – 22 May 1998, PVH, NG, CALM/SAP Survey (WAM T41933); 3 ♂, same data except 22 May – 29 September 1998, LK (WAM T44844); 1 ♀, Yelbeni, W. edge, wet pitfall trap, 31°10'24"S, 117°39'32"E, 7 September – 30 November 1999, JMW, I. Studley (WAM T42052); 2 ♂, Yorkrakine Rock Nature Reserve, site at base of rock, wet pitfall trap, 31°25'05"S, 117°30'56"E, 6 September – 29 November 1999, JMW, I. Studley (WAM T40634).



Figures 1–5 *Lycidas chrysomelas* (Simon): 1, cephalothorax and abdomen, dorsal; 2, left pedipalp, tibial apophysis, dorsal; 3, left pedipalp, ventral; 4, left pedipalp, retrolateral; 5, right leg III, retrolateral. ♂, WAM 98/1525.



Figures 6–9 *Lycidas chrysomelas* (Simon): 6, cephalothorax, lateral; 7, cephalothorax and abdomen, dorsal; 8, epigyne, ventral; 9, epigyne, dorsal. ♀, WAM 98/1526.

Diagnosis

Lycidas chrysomelas differs from all other *Lycidas* species, both described and undescribed, by the following combination of characters: male abdomen with metallic dark green/peacock blue dorsal patch with 2 ovoid black sections; male tibia III with brush of black hairs; male metatarsus III and tarsus III with brush of white hairs; males and females with two dark brown to black broad stripes extending from anterior lateral eyes to posterior of posterior lateral eyes; female with greyish border around edge of cephalothorax and with broad, short copulatory canals and reniform spermathecae.

Description

Male (WAM 98/1525)

Cephalothorax black to dark brown with lighter brown bands laterally; cephalic area with short black hairs on dark brown extending from anterior lateral eyes to edge of cephalic area; thoracic area dark brown with scattered white hairs and central strip of white hairs extending to posterior. Clypeus brown, chelicerae brown to tan distally. Maxillae, labium tan with cream edges. Anterior eyes fringed with creamy white hairs along dorsal edge. Abdomen oval in shape; dorsum of abdomen with dark green to peacock blue metallic pattern of short squamous hairs and two elongate patches of black which extend over anterior two-thirds of abdomen; brown and ginger bristles present along edges of abdomen, longer on side than posterior (Figure 1). Sternum dark brown; venter of abdomen tan with scattered greyish patches; spinnerets tan to cream with dark grey patches. Pedipalp light tan with grey patches; tibial apophysis with broad base, straight (Figure 2); proximal two-thirds of cymbium, dorsal tibia and dorsal patella of pedipalp densely covered with medium-length white hairs, distal third of cymbium with medium-length brown hairs; embolus coiled loosely, falcate, with single broad, twisted tip; tegulum not developed into posterior lobe (Figures 3, 4). Legs: femora, patella of legs I, II, III brown, femora IV, pale brown, patella IV yellow; remainder of legs I, II, IV orange with dark areas at joints; tibia III brown with brush of black hairs on dorsal and ventral sides; metatarsus III and tarsus III with brush of white hairs on dorsal and ventral sides; tarsus III brush denser dorsally and extends over tips of claws (Figure 5).

Female (WAM 98/1526)

Cephalothorax dark brown with pale yellow bands laterally and with greyish border around edge (Figure 6); cephalic area with short black hairs on dark brown extending from anterior lateral eyes to edge of cephalic area; thoracic area dark brown with scattered white hairs and central strip of white hairs extending to posterior. Anterior eyes fringed

with creamy white hairs along dorsal edge. Abdomen yellow, to creamy white, dorsum and venter speckled with greyish markings (Figure 7). Clypeus, chelicerae tan; maxillae, labium, sternum pale yellow. Spinnerets cream with grey patches. Epigyne lacking proximal receivers, fossae large, oval-shaped, accessory glands present; spermathecae large, kidney-shaped with translucent tubules overlying broad, short copulatory canals. Insemination duct openings midway along posterior edge of fossae (Figures 8, 9). Legs: femora I-IV pale yellow, remainder of all legs light brown. All leg segments with patches of grey, especially at joints.

Dimensions (mm). ♂, WAM 98/1525 (♀, WAM 98/1526): total length (excluding chelicerae) 3.63 (5.00). Carapace length 1.50 (1.81). Abdomen length 1.75 (3.12). Leg I: femur 0.69 (0.75), patella 0.44 (0.63), tibia 0.44 (0.44), metatarsus 0.37 (0.44), tarsus 0.37 (0.37). Leg II: femur 0.69 (0.75), patella 0.44 (0.56), tibia 0.44 (0.50), metatarsus 0.37 (0.44), tarsus 0.37 (0.37). Leg III: femur 1.44 (1.44), patella 0.63 (0.63), tibia 1.00 (0.94), metatarsus 0.63 (0.81), tarsus 0.44 (0.63). Leg IV: femur 0.94 (1.13), patella 0.44 (0.56), tibia 0.63 (0.75), metatarsus 0.63 (0.94), tarsus 0.50 (0.63). Legs, relative lengths: III:IV:I=II (III:IV:I:II).

Remarks

Lycidas chrysomelas occurs in semi-arid regions of mainland Australia. It ranges from semi-tropical north-western Western Australia (Drysdale River Station) to mediterranean southern Australia, and east to Finley, New South Wales (Figure 10). However, there are large gaps in the known distribution and no specimens have been recorded from the Northern Territory or Queensland but this may be due to a collection artefact. Over the past 10–15 years there has been an increase in surveying of the semi-arid areas of Australia with more emphasis being placed on the collection of invertebrates. A small spider such as *L. chrysomelas* can be easily overlooked and the majority of additional material of this species has been collected in pitfall traps. The lack of specimens from the Northern Territory, inland Queensland and central Western Australia may be due to lack of appropriate collecting and this species may yet be found in suitable parts of these areas. Collection data indicate that *L. chrysomelas* can be active at all months of the year except June and July.

Based on male pedipalpal features *L. chrysomelas* appears to be closely related to *L. nigromaculatus* (Keyserling) (Žabka, 1987) and *L. auripes* (L. Koch). Also *L. chrysomelas* female genitalia shows many features in common with *L. bitaeniatus* (Keyserling).

ACKNOWLEDGEMENTS

I thank the following people for the loan of

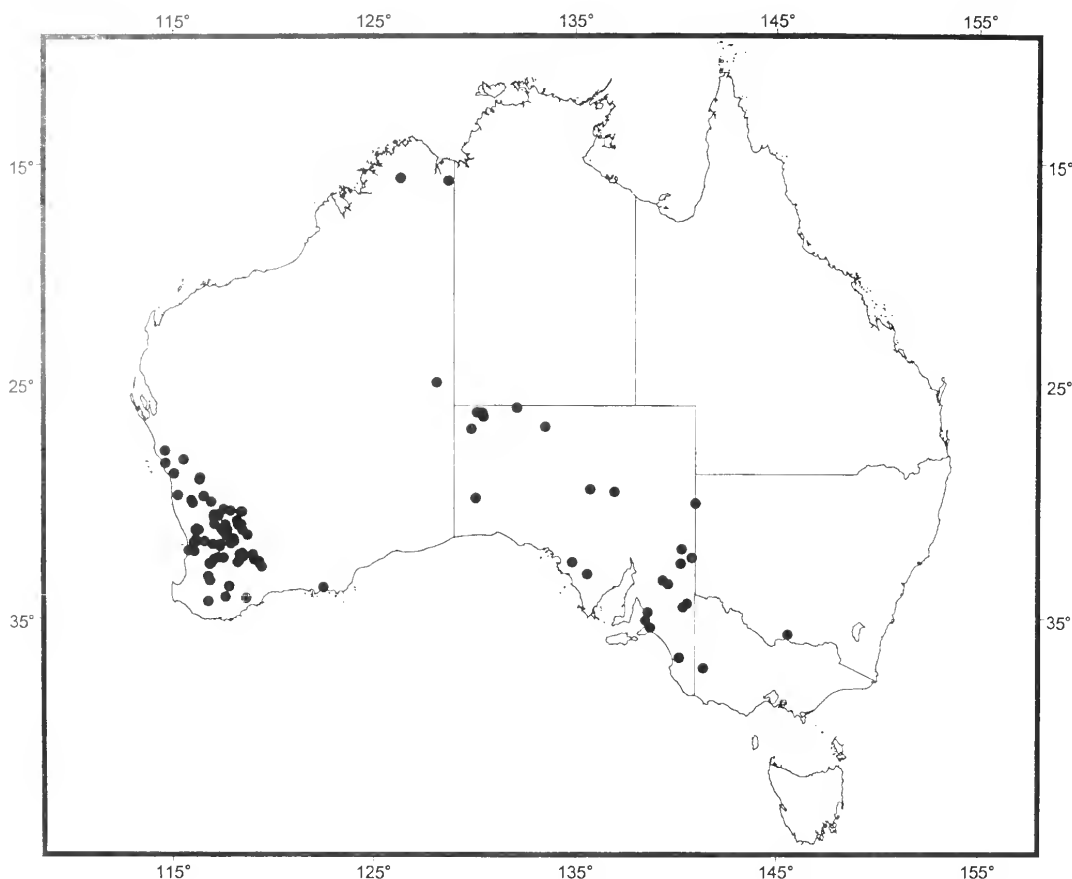


Figure 10 Map of Australia with the collection localities of *Lycidas chrysomelas* (Simon) indicated by solid circles.

material in their care: Mr D. Hirst (SAM), Dr S. Nawai and Dr J. Dunlop (ZMB), Dr A. Yen, Ms C. McPhee and Mr G. Milledge (NMV). In addition, the team involved in the collection and sorting of the spiders from the Salinity Action Plan Survey under the Conservation and Land Management Dept, W.A., in particular Mr N. McKenzie, Ms N. Guthrie and Mr P. Van Heurck. Also many thanks to Mark Harvey who encouraged me to present this description as a poster at the XIV International Congress of Arachnology, Chicago, U.S.A., 27 June – 3 July 1998 and offered valuable comments on a draft of the manuscript.

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Manuscript received 12 December 2001; accepted 20 May 2002

A systematic revision of the family Harpetidae (Trilobita)

Malte C. Ebach¹ and Kenneth J. McNamara²

¹School of Botany, The University of Melbourne, Victoria 3010, Australia.

²Department of Earth and Planetary Sciences, Western Australian Museum, Francis Street, Perth, Western Australia, 6000, Australia.

Abstract – The systematics of the ten valid harpetid trilobite genera are reviewed. Seven are revised, using standard parsimony and three-item analysis. The monophyly of the Harpetidae is confirmed, and all ingroup genera can be defended as monophyletic groups except for the non-monophyletic *Scotoharpes* group. Emended diagnoses are provided for all the genera within the family. The three subfamilies Dolichoharpinae, Eoharpetinae and Harpetinae are suppressed within the Harpetidae. The genera *Australoharpes* and *Sinoharpes* are placed in synonymy with *Dubhglasina*. *Thorslundops* and *Wegelinia* are placed in synonymy with *Hibbertia*, and the subgenus *Fritchaspis* placed in synonymy with *Lioharpes*. *Reticuloharpes* and *Helioharpes* are placed in synonymy with *Harpes*. The Harpetidae, along with the Entomaspidae and Harpididae, is considered to belong in the Harpetida, which is herein raised to ordinal rank within the subclass Libristoma.

INTRODUCTION

The trilobite family Harpetidae Hawle and Corda, 1847 has been revised twice since its erection over 150 years ago, firstly by Whittington (1950a) and secondly by Přibyl and Vaněk (1986). Subsequently, numerous authors (Prantl and Přibyl, 1954, Vaněk, 1963, Přibyl and Vaněk, 1981, Přibyl and Vaněk, 1986) have left a legacy of what we regard as unnecessary subfamilies, poorly supported genera, subgenera, species and subspecies. The most recent revision by Přibyl and Vaněk (1986), perhaps the most detailed to date, indicates the enormity of the task involved in clearing up this 'Harpetid legacy'. For instance, one case relates to the subfamilies Dolichoharpetinae, Eoharpetinae and Harpetinae, which Přibyl and Vaněk (1981) proposed. Each subfamily, however, is loosely supported by spurious characteristics that also define members of the other subfamilies. The Harpetidae should stand alone as a monophyletic group, or as several related clades supported by more than two or three synapomorphies each. Moreover, the past practice of assigning poorly preserved single specimens to new species and genera is unacceptable.

This is the first cladistic analysis undertaken of the Harpetidae. The result is that the Harpetidae are characterised by synapomorphies rather than by either ancestor-descendant or biostratigraphic relationships. Of the previously described genera, seven were subjected to a cladistic analysis of their internal relationships: *Bohemoharpes* Vaněk, 1963, *Dubhglasina* Lamont, 1948b, *Eoharpes* Raymond, 1905, *Harpes* Goldfuss, 1839, *Hibbertia* Jones and

Woodward, 1898, *Lioharpes* Whittington, 1950a and *Scotoharpes* Lamont, 1948a. Not included within this analysis were *Brachyhipposiderus* Jell, 1985 and *Dolichoharpes* Whittington, 1949, because each contain too few species to enable a cladistic analysis to be carried out. A cladistic analysis of *Kielania* Vaněk, 1963, along with a new genus, will be presented elsewhere (Ebach and McNamara, in prep.).

Three-item analysis is used as the favoured cladistic method (Williams and Siebert in Scotland and Pennington 2000). However, due to the implementation of the three-item method, standard parsimony is included for comparison. Because of the large degree of morphological variability encompassed by the species within each genus, any cladistic analysis dealing with supraspecific taxonomy must be treated with caution.

METHODS

In cladistics it is possible to construct cladograms using different methods. The most common method is standard parsimony analysis. The character-states in standard parsimony are treated as a transformation series, i.e., one state transforming into another. Although the use of transformation series has its merits, its premise of transformations is a pre-cladistic concept (Kitching *et al.* 1998). In order to move away from the 'established' standard parsimony analysis and into a realm in which character-states are treated as taxa (by degrees of relationship), three-item analysis is considered to be

the most appropriate method to use. Three-item analysis finds a suite of the smallest units of relationship, a three-item statement, for each character (Nelson and Platnick 1991). A series of three-item statements is converted into a binary matrix and can then be processed using any standard parsimony program.

Three programs are necessary to implement a three-item analysis. MATRIX (Nelson and Ladiges 1995) converts the matrix into a three-item matrix. TAX (Nelson and Ladiges 1995) then applies weights (factor = 50) to each statement (see also Kitching *et al.* 1998). NONA 2.0 (Goloboff 1998) (max. trees = 100; mult* = 1000; trees per rep = 20, TBR branch swapping), finds the most parsimonious trees. NONA excludes any ambiguous optimisations (i.e., ACCTRAN), and is the best mechanical way of finding the minimal tree (Williams 1996). Standard parsimony analyses are run using the same settings in NONA as in the three-item analysis and included for comparison.

Character states are optimised onto standard parsimony and three-item trees using WINCLADA version 0.9 (Nixon 1999). Characters optimised onto standard parsimony trees give inference to character transformations on the first tree. The first is chosen by default for each analysis. Optimised character states on three-item minimal trees provide no information regarding character transformations due to the nature of implementation (see Kitching *et al.* 1998: 167-186).

The characters coded for cladistic analysis were taken from both specimens and photographs. Specimens were painted with carbon, and then coated with ammonium chloride, in order to attain high quality, contrasting photographs.

SYSTEMATIC PALAEONTOLOGY

Terminology

Cephalic nomenclature used herein follows Whittington (1950a, fig 1, 1959, fig. 85, 1997). However, it should be noted that in Whittington (1959, fig. 85) there are two inaccuracies, arising from the redrawing of Whittington (1950a, fig.1). The line for the brim prolongation is too long, and points to the genal roll prolongation. The line for the genal roll prolongation is too short and points to the internal rim of the prolongation, rather than to the genal roll prolongation.

Due to the unique cephalic features of harpetids and the ambiguity of some of the terms, a revised version of cephalic features is given in Figure 1 herein. In this revision it is essential to introduce some new terms to cover morphological features that have not been previously named. These are:

- *Girder kink* – a sagittal deflection of the girder,

resulting in either an anteriorly convex deflection, or a posteriorly convex deflection;

- *Anterior boss* – a sagittal inflation that may extend from the prelabellar field onto the genal roll, and sometimes onto the brim;
- *Sagittal crest* – a narrow ridge that extends sagittally along the glabella, and effaces posteriorly;
- *Transverse prelabellar ridge* – occurs as a raised, non-tuberculate region immediately anterior (sag.) to the prelabellar furrow, or as a ridge that is continuous with the eye ridge;
- *Alar ridge* – secondary furrow running parallel to axial and alar furrows, forming prominent ridge;
- *Interalar furrow* – an exsagittal furrow traversing the ala;
- *Alar depression* – a depressed area anterior to the ala, adaxial to axial furrow;
- *Posterior alar depression* – depressed area posterior to ala, proximal to posterior border.

Function of the Harpetid Brim

The harpetid brim has been described variously as functioning like a plough (Dollo 1909, Staff and Reck 1911), as a sieving or hydrostatic device (Rouault 1847, Richter 1920), or as a strengthening and lightening function (Miller 1972), or as a respiratory (Jell 1978) or sensory organ (Whittington 1950a). Despite the very variable interpretations, they do highlight the significance of the coarse pitting and/or caeca as being the primary functional organs of the fringe. With this assumption in mind, the presence of both pits and caeca on the brim indicate a functioning brim. Coarse pitting and caeca are herein regarded as being both a valid structure for cladistic analysis and as a possible 'functional organ'. Fine pitting or granules do not serve as homologous functional organs and are herein defined as 'ornament'.

Material

Figured specimens used in this study are held as follows: GLAHM, Hunterian Museum, Glasgow, U.K.; MBT, Museum of Natural History, Humboldt University, Berlin, Germany; Department of Palaeontology, Natural History Museum, London, U.K.; NIGP, Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China; NM, Department of Palaeontology, National Museum, Prague, Czech Republic; NMV, Department of Invertebrate Palaeontology, Museum Victoria, Melbourne, Australia; SM, Senckenberg Museum, Frankfurt, Germany; ÚÚG, Czech Geological Survey, Prague, Czech Republic; WAM, Department of Earth and Planetary Sciences, Western Australian Museum, Perth, Australia.

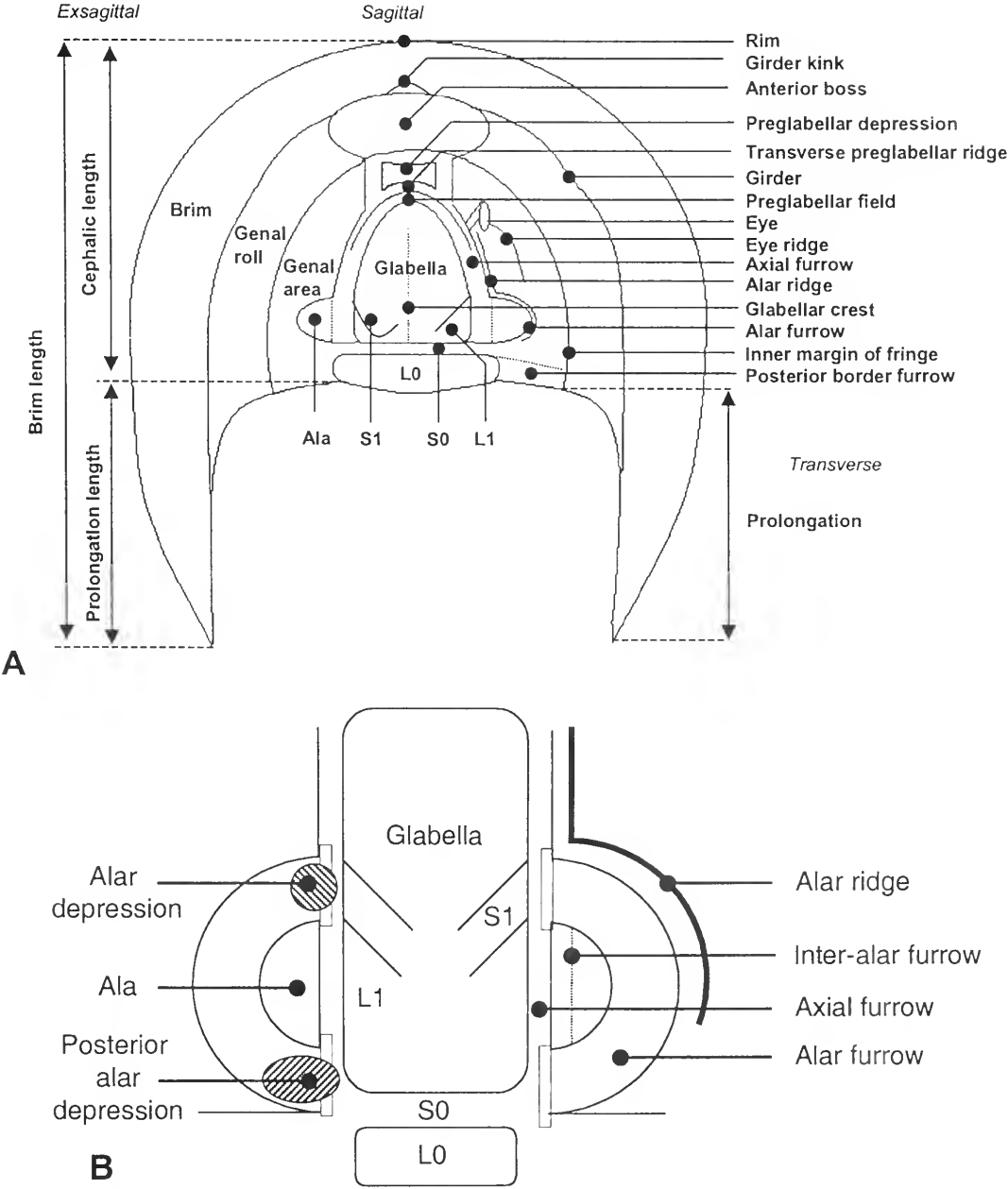


Figure 1 A, Schematic diagram of a harpetid cephalon. B, Nomenclature of the alae.

Class Trilobita Walch, 1771
Subclass Libristoma Fortey, 1990
Order Harpetida Whittington, 1959
Harpina Whittington, 1959: 415

Emended Diagnosis
Cephalon semicircular to ovate. Fringe inclined, consisting of vaulted inner genal roll, which is convex or flat, and an outer bilamellar brim, which is either flat, convex or concave; extends posteriorly to prolongation. Glabella anteriorly tapering, with

one to three pairs of lateral glabellar furrows; preoccipital pair isolate triangular lateral lobes. Alae may be present. Genae convex; preglabellar field posterior to vaulted (in lateral view) genal roll. Prominent eye lobes or tubercles centrally located on genae, with well-defined eye ridges and in some forms with genal ridge. Suture marginal. No rostral plate. Radiating, anastomosing caecae may be present on genae, and preglabellar field, extending onto fringe prolongations. External surface of cephalon may be tuberculate or granulose. Thorax with 12 or more segments; pleurae flattened, with broad axial furrows. Pygidium elongate to short, subtriangular.

Remarks

Whittington (1959: O415) erected the Harpina as a suborder of the Ptychopariida Swinnerton, 1915 on the basis of the unique characteristics of the fringe and cranidium. While the semicircular to ovate, bilaminar fringe, with extensive pitting and caeca are indeed unique, they are, moreover, absent in all other suborders of the Ptychopariida. Fortey (1990) erected the Libristoma to act as a high level monophyletic group that equates with the Order Ptychopariida. The consequences are two-fold: either the Ptychopariida is renamed the Libristoma, or is proposed as a subclass consisting of all ptychopariid orders and suborders. The Libristoma is herein regarded as a subclass, as preferred by Fortey (1990: 558). The authors agree with Fortey (1990: 558) that the Subclass Libristoma will not upset current classification within the Ptychopariida and will need to be subjected to a cladistic analysis to assess monophyly of its orders. Fortey (1990), however, is sceptical that the subclass Libristoma will not be used as with many other higher-level taxonomic classifications in the past (see Stubblefield 1936, Harrington 1959, Bergström 1973 and Fortey and Owens 1975). Many higher-level taxonomic revisions are often ignored, but this should not stop the reform of redundant taxonomic groups.

Fortey (1990) kept the possibility of subclass Libristoma open and retained all orders and suborders in their traditional taxonomic rank. The adoption of Fortey's Libristoma, however, does have consequences on the taxonomic status of the Harpetida. Fortey and Chatterton (1988) and Fortey (1990) pointed out that two of the diagnostic characters of the Ptychopariida are the presence of a rostral plate and opisthoparian facial sutures. All members of the Harpetida lack a rostral plate and have a marginal facial suture. Consequently, the Harpetida is herein raised to ordinal status and is considered to be a monophyletic group within the Subclass Libristoma.

The Harpetida contains three families, the Harpetidae Hawle and Corda, 1847, Harpididae,

Whittington 1950a and Entomaspididae, Ulrich *in* Bridge 1930. This latter family Ludvigsen (1982) placed within the superfamily Solenopleuracea (see Fortey 1990: 562). However, Fortey (1990) has pointed out that there is no justification for retention of the superfamily Solenopleuracea.

The nomenclatural change from the Harpina Whittington, 1959 to the Harpetida is a result of the highlighting by Beu (1971: 56) of the homonymy between Harpidae Hawle and Corda, 1847 in the Trilobita and Harpidae in the Mollusca (see also Rheder 1972: 2; Chernohorsky 1972: 108; Rheder 1973: 3). The Harpetidae Hawle and Corda, 1847 and Harpididae Whittington, 1950a were placed on the Official List 'Names in Zoology' Opinion 1436 (1987: 137).

The Harpetida has an extensive evolutionary and geological history, spanning the Upper Cambrian to the Late Devonian (Frasnian). In the Early Ordovician, the ancestral Harpetidae lost the prominent ptychopariid-like sutures and gained the long prolongations typical of the Harpididae and Entomaspididae. However, the unique harpetid morphological characteristics and evolutionary history let them stand alone as a monophyletic group.

Family Harpetidae Hawle and Corda, 1847

Arraphidae Angelin, 1854: 21.

Harpidae Hawle and Corda, 1847; Beu 1971: 56; Rheder 1972: 2; Chernohorsky 1972: 108; Rheder 1973: 3; Přibyl and Vaněk 1986: 15; Opinion 1436 1987: 137.

Emended Diagnosis

Bilamellar fringe with opposed pits on outer surfaces. Genal roll steeply sloping; girder well-defined and may extend onto prolongation. Prolongation straight to incurving, of variable length. Alae semicircular adjacent to posterior glabellar lobes where present. When pits are present, concentrated on girder and rim. Hypostome pear-shaped in outline with ovate middle body, large anteriorly and small posteriorly. Thorax with 12–21 segments. Pygidium small, short (sag.), triangular, with few segments.

Remarks

Přibyl and Vaněk (1986) assigned the Harpetidae to the Conocoryphacea Angelin, 1854 due to a 'hypothetical congruent link' based on a high number of thoracic segments, small pygidium and the homologous shape of the hypostome, totally ignoring the presence of the fringe that only occurs within the Harpetidae. Přibyl and Vaněk's (1986) 'hypothetical' link is unsubstantiated and too unspecific to justify the synonymy. Herein the

Harpetidae is considered to be a distinct, recognisable, monophyletic taxon that may share a close relationship, but is in no way grouped within the Conocoryphacea.

Whittington's (1959) emended diagnosis of the Harpetidae had been subsequently changed by Příbyl and Vaněk (1981) who split the family into three subfamilies: the Dolichoharpetinae, Eoharpetinae and Harpetinae. Příbyl and Vaněk (1986: 22) established the Eoharpetinae for genera with semicircular or semi-elliptical, smooth, sometimes depressed alae below the level of genal lobes and eye ridges, and which do not show any 'close phylogenetic relationships to other Harpetid subfamilies'. A major problem with this grouping is that it is not based on any distinct characters. 'Semicircular' to 'semielliptical' or 'sometimes depressed ala' are vague, hard to define terms and occur in other genera (*Dolichoharpes*) that they did not place in the Eoharpetinae. Their claim that the Eoharpetinae shows no close phylogenetic relationships to other Harpetidae is a *non sequitur* as they placed them in the same family. Another poorly described subfamily is the Dolichoharpetinae Příbyl and Vaněk, 1981: 191. This was based on the generic characters of its only included genus, *Dolichoharpes*. There seems little justification in this case to erect a subfamily on the basis of this single genus, especially given that this genus shares the diagnostic characters of the Eoharpetinae.

The third subfamily, the Harpetinae, was erected by Příbyl and Vaněk (1981: 191) on the basis of a cephalon with brim horseshoe-like to pyriform in outline, depressed alae and concave brim (Příbyl and Vaněk 1986: 15). Their diagnosis suffers similarly from descriptions of characters that are variable at species level, for instance, the Eoharpetinae, are defined on 'alae usually not depressed' and 'brim concave'. Both these characters are variable within several genera of the Harpetinae (*Scotoharpes*, *Hibbertia* and *Bohemoharpes*). The Dolichoharpetinae, Eoharpetinae and Harpetinae do not include whole genera, rather they represent characteristics that can be attributed to any number of taxa from a varying number of genera. All three subfamilies are considered non-monophyletic herein.

It should also be noted that recent reviews by Owen and Clarkson (1992) and Lespérance and Weissenberger (1998) place *Platyharpes* Whittington, 1950b and *Paraharpes* Whittington, 1950b in synonymy with *Hibbertia* Jones and Woodward, 1898.

Genera Included

Bohemoharpes Vaněk, 1963; *Brachyhipposiderus* Jell, 1985; *Dolichoharpes* Whittington, 1949; *Dubhglasina* Lamont, 1948a; *Eoharpes* Raymond, 1905; *Harpes* Goldfuss, 1839 [= *Helioharpes* Příbyl and Vaněk,

1981 and *Reticuloharpes* Vanek, 1963]; *Hibbertia* Jones and Woodward, 1898 [= *Metaharpes* Lamont, 1948a, *Platyharpes* Whittington, 1950a and *Paraharpes* Whittington, 1950a, *Harpesoides* Koroleva, 1978]; *Kielania* Vaněk, 1963; *Lioharpes* Whittington, 1950a; *Scotoharpes* Lamont, 1948b; *Thorshundops* Příbyl and Vaněk, 1981; *Wegelinia* Příbyl and Vaněk, 1981.

Genus *Bohemoharpes* Vaněk, 1963

Figure 2A

Bohemoharpes (*Unguloharpes*) Příbyl and Vaněk, 1981: 188.

Bohemoharpes (*Declivoharpes*) Příbyl and Vaněk, 1981: 188.

Type Species

Harpes naumanni Barrande, 1852 from the Silurian of Bohemia.

Emended Diagnosis

Oval or semicircular shaped brim; flat to concave, finely pitted with caeca; girder kink concave (sag.) in plan view. Glabella and genal area vaulted, S1 deep, L1 subtriangular; alae small and subdued; occipital ring with median tubercle. Thorax up to 26 segments, pleurae tapering laterally with wide interpleural furrow.

Remarks

The large number of subgenera proposed by Příbyl and Vaněk (1981) within the Harpetidae is unwarranted. *Bohemoharpes* (*Declivoharpes*) was erected on several trivial characters that include a "narrower (sag.) brim of horse-shoe shaped and smaller alae and a well perceptible pair of muscle scars near the preoccipital pair of axial furrows" (Příbyl and Vaněk 1981: 188), that are missing in most species. *Bohemoharpes* (*Unguloharpes*) was also diagnosed using characteristics variable with the proposed subgenera, but contained within the genus. These include such characters as a "brim which is broad, almost flat, obliquely sloping forwards, by carinate glabella and relatively large alae." Neither of the above diagnoses are substantial enough to warrant a new subgenus, especially on characters such as muscle scars, that vary little between species and are only preserved in a handful of specimens. The subgenera *Declivoharpes* and *Unguloharpes* are not recognized herein.

Bohemoharpes was erected on the basis of the possession of a "distinctly concave brim". This single characteristic is absent in *Harpes praecedens dvorcensis* Prantl and Příbyl, 1954, which was subsequently placed in *Bohemoharpes*. This species has a raised and flat to convex brim. *Harpes praecedens* was later assigned to *B. (Declivoharpes)* by

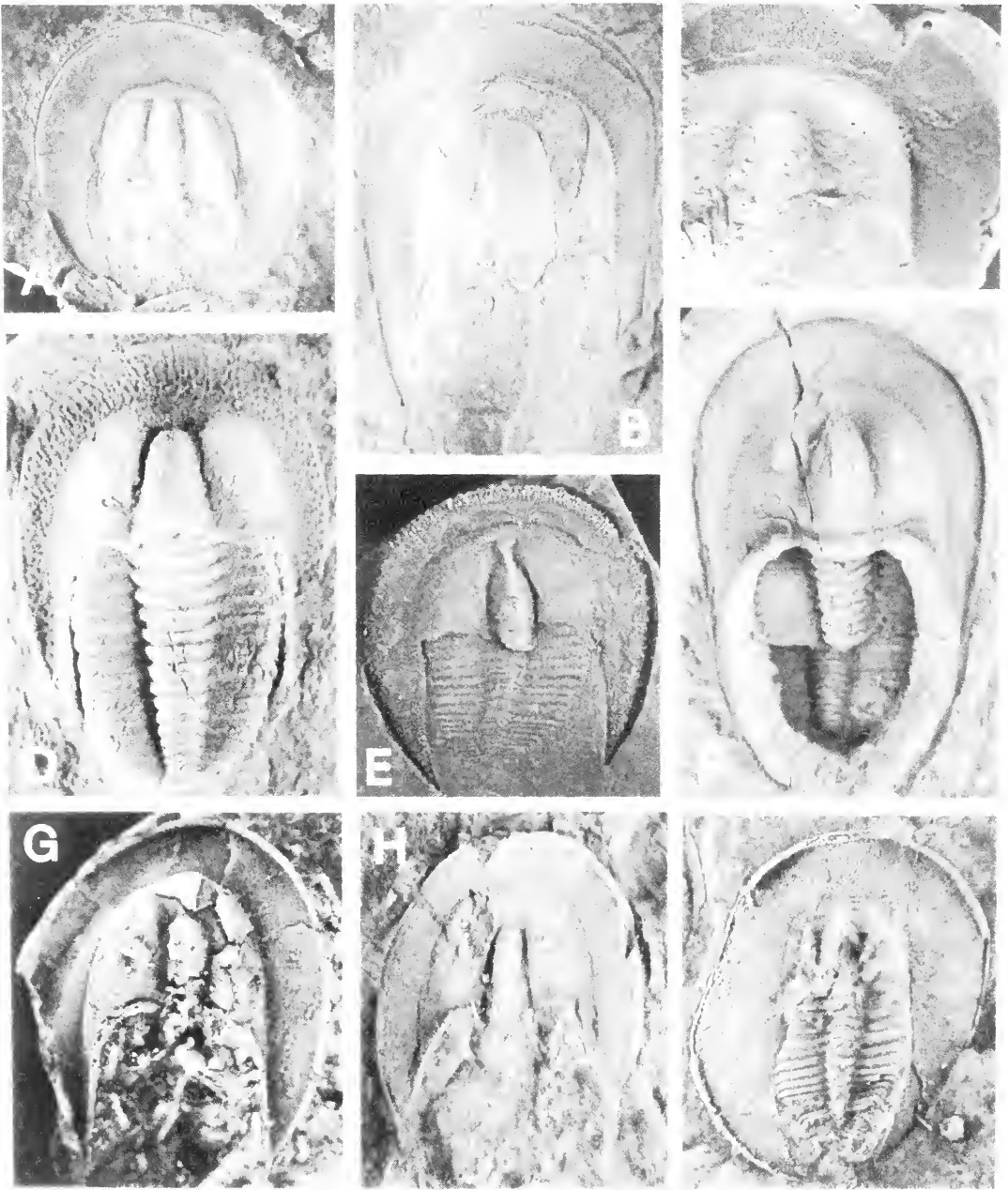


Figure 2 A, *Bohemioharpes naumanni*, external mould, dorsal view of cephalon NM L6127. B, *Lioharpes venulosus*, internal mould, dorsal view of cephalon NM L12547. C, *Scotoharpes tatouyangensis*, internal mould, dorsal view of cephalon NI 10131. D, *Eoharpes primus*, external mould, dorsal view of exoskeleton NM Coll. Kloucek No. 48. E, *Harpes radians*, internal mould, dorsal view of cephalon, MBT 4512. F, *Harpes perradatus*, external mould, dorsal view of exoskeleton, WAM 01.356. G, *Scotoharpes singletoni*, internal mould, dorsal view of cephalon, NMV P74430. H, *Brachylipposiderus secundus*, internal mould, dorsal view of cephalon, holotype NIGP 108245. I, *Hibbertia balclatchiensis*, internal mould, dorsal view of cephalon IN 43838.

Příbyl and Vaněk (1986). However, the strongly raised and gently convex brim and the fineness of brim perforations are more characteristic of *Kielania* Vaněk, 1963. Although Vaněk (1963) and Ormiston (1973) both mention steep genal prolongations as a unifying character of *Kielania*, the absence of preserved prolongations in *H. praecedens* does not mitigate against its inclusion within *Kielania*. Consequently, *Bohemoharpes praecedens* is herein assigned to *Kielania*.

Species Included

Harpes acuminatus Lindström, 1885; *Bohemoharpes bubovicensis* Příbyl and Vaněk, 1986; *H. buphthalmus* Novák, 1890; *H. gracilis* Münster, 1840; *B. hypsipyle* Příbyl and Vaněk, 1986; *B. inflexa* Doubrava, 1991; *B. janae* Doubrava, 1991; *H. naumanni* Barrande, 1852; *H. ovatus* Bouček, 1935; *H. ungula* Sternberg, 1833; *H. vittatus* Barrande, 1852; *H. wilkensisii* Münster, 1840.

Bohemoharpes wilkensisii (Münster, 1840)

Harpes wilkensisii Münster, 1840: 1.
Bohemoharpes wilkensisii (Münster, 1840); Příbyl and Vaněk 1986: 16, text-fig 8, figs 3–4.
Harpes crassifrons Barrande, 1846: 5; Prantl and Příbyl 1954, pl. 3, fig. 4, pl. 8, fig. 1.
Bohemoharpes crassifrons Vaněk, 1963: 227; Příbyl and Vaněk 1986: 16, text-fig 2, figs 1–2.

Material

Bohemoharpes wilkensisii (holotype ÚÚG JV 432) from the upper Silurian, Elbesreuth, Germany. *Bohemoharpes crassifrons* (holotype NM L 6128) from the Wenlock, Motol Member, Liteň Formation, Kozel near Beroun, Bohemia, Czech Republic.

Discussion

Barrande (1846) erected *Harpes crassifrons* as a new species based on several incomplete specimens that share similar characteristics with *Bohemoharpes wilkensisii* (Münster, 1840). The characters shared by both species include a strongly inflated genal roll, concave and perforated brim and ovoid fringe. *Harpes crassifrons* is herein considered a junior subjective synonym of *B. wilkensisii*.

Cladistic analysis

Outgroups

Eoharpes was used as an appropriate outgroup for the *Bohemoharpes* analysis. The better known and preserved *E. benignesii* (Barrande, 1872) was used in place of the poorly preserved type species *E. primus* Raymond, 1905. The characters possessed by *Eoharpes*, such as the vaulted glabella and palpebral

Table 1 Data matrix for *Bohemoharpes*. ‘?’ indicates missing data.

	0	1	2	3	4	5	6	7	8	9
<i>Eoharpes</i>	0	0	0	1	0	0	0	0	0	?
<i>B. bubovicensis</i>	?	?	?	0	1	0	1	1	0	?
<i>B. buphthalmus</i>	0	0	1	1	0	1	1	0	1	?
<i>B. hypsipyle</i>	0	1	1	1	0	0	0	0	0	?
<i>B. inflexa</i>	0	0	1	1	1	1	1	0	0	1
<i>B. janae</i>	0	1	1	0	1	1	1	0	0	0
<i>B. naumanni</i>	1	0	0	0	1	1	?	0	0	1
<i>B. ovatus</i>	0	1	1	1	1	0	1	0	0	1
<i>B. ungula</i>	0	1	1	2	1	0	1	0	0	0
<i>B. vittatus</i>	0	1	1	1	1	0	1	1	1	0
<i>B. wilkensisii</i>	1	0	1	0	0	?	1	0	1	1

lobes, and small alae, are characteristic of the earliest known *Bohemoharpes* species including *B. naumanni* and *B. wilkensisii*.

The following ten *Bohemoharpes* characters are listed as a data matrix in Table 1.

Characters

0. Brim shape. The *Bohemoharpes* brim falls in two broad categories, semicircular and circular.
0: semicircular; 1: circular

1. Brim concavity. Measured as the mid-brim concavity (sag.). The brim of *Bohemoharpes* is usually concave along the prolongation or lateral to the posterior border. Species with sagittal brim concavity tend to have overall brim concavity. *Eoharpes* has little sagittal concavity, thus state 0 is considered primitive.
0: flat or convex; 1: concave along whole margin

2. Girder kink. The kink is an independent character that is caused by either an increase in the anterior extent of the axial furrows and an increase in the size of the anterior boss, or an increase in genal roll convexity, as in *B. wilkensisii*. The absence of the kink in *Eoharpes* is considered primitive.
0: absent; 1: present

3. Course of inner margin of fringe. The course of the inner margin of the fringe can be influenced by the presence of deep anteriorly extended axial furrows on the genal roll. Convexity (in dorsal view) is unusual and most inner margins are either straight or concave. *Eoharpes* codes as state 1.
0: straight or convex 1: concave

4. Condition of preglabellar furrow (sag.). Preglabellar furrow length (sag.) is measured against axial furrow width (tr.). A long preglabellar furrow is usually shallow and at times limits the anterior extent of the axial furrows. Preglabellar length is measured sagittally directly anterior to the frontal

lobe. Any wide (sag.) furrow anterolateral to the frontal lobe should be coded as state 0.

0: wide; 1: narrow

5. *Eye ridge*. A distinct eye ridge is outlined by two furrows to form a raised ridge. Species that show only one furrow or a faintly inflated ridge should be coded as 1.

0: ridge present; 1: faint inflation to absent

6. *Shape of S1*. Posterolaterally directed furrows are plesiomorphic to 'J' shaped furrows. 'J' shaped furrows are not continuous with S0.

0: posterolaterally directed; 1: 'J' shaped

7. *Alar inflation*. Alae are either flat or inflated. Alae are not inflated in *Eoharpes*, thus 7: 0 is considered plesiomorphic.

0: absent; 1: present

8. *Alar shape*. Alae are either transversely or anterolaterally directed, long axis inclined at 45° to a transverse line. Alar shape varies in most harpetid genera including *Bohemoharpes*. Alae are always transversely directed in *Eoharpes*.

0: transversely directed; 1: anterolaterally directed

9. *Prolongation concavity*: Measured as the outward concavity of the whole inner margin. All species of *Bohemoharpes* are concave at the anterior-most part

of the inner margin of prolongation. A distinctly concave inner margin has the same concavity along the whole margin.

0: straight; 1: distinctly concave

Results and Discussion

Standard parsimony analysis yielded an unresolved consensus of 34 trees (length=31, ci 31, ri 35). Three-item analysis yielded a minimal tree (length=4666, ci 73, ri 64) (Figure 3).

The cladistic analysis is consistent with the taxonomic synonymy of *B. (Declivoharpes)* and *B. (Ungloharpes)* into *Bohemoharpes* as there are no clades to justify such sub-divisions. The development of the 'J'-shaped, posterolaterally directed S1 [6: 1] appears to have occurred early in *Bohemoharpes* phylogeny. The other significant homologies that have resulted in two distinct groupings are the development of narrow prelabellar furrows [4: 1], absent in *B. buphthalmus*, *B. wilkensis* and *B. hypsipyle*, and alar inflation [7: 1] in *B. bubovicensis* and *B. vittatus*.

The Lochkovian *Bohemoharpes hypsipyle*, the youngest member of *Bohemoharpes*, is basal to all Silurian species. *Bohemoharpes* is monophyletic and consists of two distinct clades, *B. buphthalmus*, *B. wilkensis* and *B. naumanni*, *B. inflexa*, *B. janae*, *B. ungula*, *B. ovatus*, *B. bubovicensis* and *B. vittatus*.

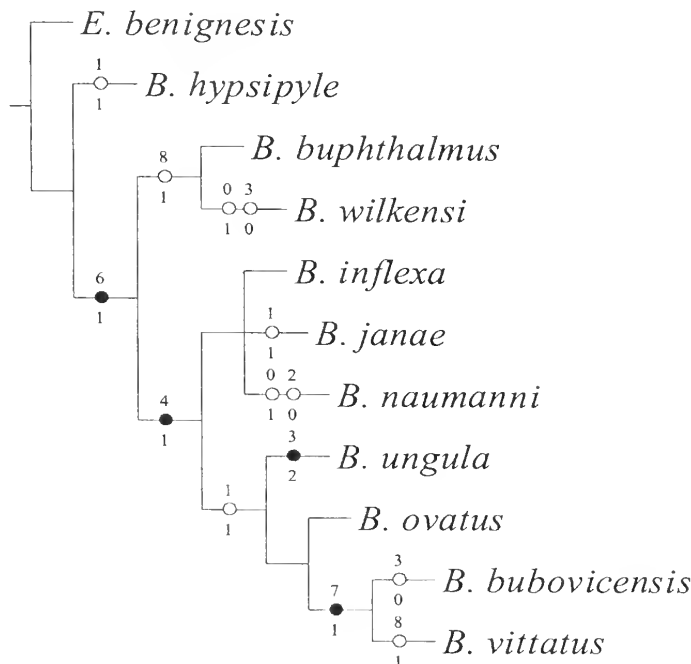


Figure 3 Three-item analysis of *Bohemoharpes* found a minimal tree of two trees (length = 4666, ci 73, ri 64).

Genus *Brachyhipposiderus* Jell, 1985

Figure 2H

Type Species

Brachyhipposiderus loginus Jell, 1985, from the Lancefieldian (Tremadoc) Digger Island Formation, Waratah Bay, Victoria, Australia.

Emended Diagnosis

Cephalon semicircular; brim flat to concave; alae small, depressed; axial furrows deep; caeca radial, anastomosing on genae and brim, interspersed with large pits; prolongations short, with well-defined spine.

Remarks

Brachyhipposiderus is the earliest known harpetid. It ranges from the Upper Cambrian-Lower Tremadoc Panjiazui Formation, Hunan Province, China to the Tremadoc Digger Island Formation, Victoria, Australia and Madaoyu Formation, Hunan Province, China.

Jell (1985: 71) described *Entomaspis* as 'giving rise to the harpetids' based on the "radial pitting of the brim, lower overall cranial convexity, strongly developed girder, weakly developed alae, and glabellar and palpebral organisation of *Brachyhipposiderus*". However, one can argue that *Harpides* Beyrich, 1846 has equal ancestral claim, based on strongly anatomising caeca and weakly developed alae in *Brachyhipposiderus*.

A brief revision by Peng (1990: 110) considered *Scotoharpes planilimbatus* (Lu, 1975) to be a member of *Brachyhipposiderus*. The wide, flat, heavily pitted brim, long prolongation spines and strong palpebral caeca are attributes common to both genera. However, because this species is only known from a brim, it is not possible to be certain that it has all the attributes of *Brachyhipposiderus*. Consequently, *S. planilimbatus* is retained in *Scotoharpes*.

Species Included

B. secundus Peng, 1990.

Brachyhipposiderus secundus Peng, 1990

Scotoharpes? hunanensis Peng, 1984: 380.

Material

NIGP 108250 figured in Peng (1984, pl. 17, figs 1, 2). NIGP 108245-9 figured in Peng (1990, pl. 20, figs 1-5).

Discussion

Brachyhipposiderus hunanensis was described from a "single poorly preserved internal mould of cephalon" (Peng 1990: 109). This specimen was

initially placed in *Scotoharpes*, however, the "short transverse triangular-shaped prolongation, the sturdy genal spine and strong girder" (Peng 1990: 109) suggest that it belongs in *Brachyhipposiderus*. The incomplete cephalon of the type specimen and the narrow brim, wide cephalon and small size of the specimen figured in Peng (1990, pl. 20, fig 6), indicate that it is a juvenile specimen, possibly of *B. secundus*. Peng (1990), however, believed *B. secundus* to be "morphologically different" based on "proportionally longer prolongations [and] more posteriorly placed girder [that] meets the internal rim more anteriorly to the tip of the prolongation" (Peng 1990: 110). The morphological difference between both species is based on slight variation in the girder and prolongation. The difference in age is used to define species as *B. secundus* is "stratigraphically younger than the earlier *B. hunanensis*" (Peng 1990: 110). However, differences in age or biogeography are not valid characters to use in the characterisation of a species. Consequently, *B. hunanensis* is considered to be a junior subjective synonym of *B. secundus*.

Genus *Dolichoharpes* Whittington, 1949

Type Species

Eoharpes uniserialis Raymond, 1925.

Emended Diagnosis

Cephalon ovate, strongly convex, with short median and anterior lateral glabellar furrows; alae large and deeply depressed below rest of genae; girder extending to tips of very long prolongations; brim narrow; coarse reticulate ornament on fringe and genae; glabellar lobes large, with curved ridge.

Remarks

Dolichoharpes is the most distinctive harpetid genus, and yet it is the hardest to distinguish at species level. Since Whittington's (1949) erection of the genus, doubt over the establishment of several new species was expressed by DeMott (1963) and Shaw (1968) (see Chatterton and Ludvigsen 1976). DeMott (1963) synonymized three species (*Dolichoharpes escanabe* (Hall, 1851), *D. dentoni* (Billings, 1863), *D. rutrellum* (Clarke, 1897)) with *D. uniserialis*, and Shaw (1968) synonymized *D. proclivius* Esker, 1964 and *D. arcticus* Whittington, 1954 with *D. reticulata* Whittington, 1949. The remaining species, *D. doranni* Whittington, 1950a and *D. villosus* Koroleva, 1978 are based on fragmentary specimens, too poor to use for cladistic analysis. In the discussion on *D. aff. reticulata*, Chatterton and Ludvigsen (1976: 43) noted that the characters used to separate North American species were variable, a problem that is common to all species

of *Dolichoharpes*. The single incomplete internal mould of *Dolichoharpes villosus* from the Ordovician of North Kazakhstan (Korovela 1978), is distinguished by indeterminate characters. These include 'basal furrows on the glabella', gently sloping anterior region and narrow convex glabellar lobes (Koroleva 1978: 219). The characters distinguishing *D. villosus* are found in most *Dolichoharpes* specimens from North America (Chatterton and Ludvigsen 1976; Shaw 1968).

More specimens of *Dolichoharpes* need to be found before a thorough taxonomic and cladistic study of *Dolichoharpes* can be made. This reiterates the sentiment already voiced by Whittington (1950a: 30) and Chatterton and Ludvigsen (1976).

Species Included

Dolichoharpes doranni Whittington, 1950a; *D. reticulata* Whittington, 1949; *D. villosus* Koroleva, 1978; *D. sp.* Chatterton and Ludvigsen 1978; *D. sp.* (Shaw 1968); *D. sp.* (Dean 1979); *D. sp.* (Přibyl and Vaněk 1981).

Cladistic Analysis

Outgroups

There are no known harpetid genera that exhibit the unique features of the cephalon and extremely long prolongations of *Dolichoharpes*. The mid Ordovician genus is contemporary with most Ordovician harpetid genera, such as *Scotoharpes*, *Eoharpes* and *Hibbertia*. However, *Eoharpes* and *Brachylipposiderus* are potential outgroups for a future cladistics analysis. Their characters, such as the narrow brim in *Brachylipposiderus* and the development of prolongations and ornament in *Eoharpes*, are possibly plesiomorphic.

Characters

Whittington (1949: 281) noted the character that best distinguished *D. reticulata* from *D. uniserialis* was the detail of the fringe. Even in the complete silicified specimens of *D. aff. reticulata* described by Chatterton and Ludvigsen (1976), the fringes themselves exhibit little detail of the girder or inner margin due to coarse pitting.

Whittington (1950a), however, suggested that *D. doranni* is closely related to the North American species because it does not possess "the ridge crossing the first glabellar lobes or the less strongly ornamented oval areas of the second lobes." (Whittington 1950a: 29–30). This is perhaps the only suggestion possible given the poor detail in the majority of specimens.

Genus *Dubhglasina* Lamont, 1948b

Figure 4

Australoharpes Harrington and Leanza, 1957: 195.

Sinoharpes Sheng, 1974: 105; Tripp *et al.* 1989: 47.

Type Species

Harpes parvula M'Coy, 1851: 387, from the Caradoc (Middle Ordovician) *Didymograptus superstes* Mudstones, near Girvan, Ayrshire, Scotland.

Emended Diagnosis

Cephalon oval in outline, low in convexity. Girder extending to tip of prolongations; genal roll narrow; brim broad and flattened. Small posterior lateral glabellar lobes. Preglabellar furrow and preglabellar field elevated, laterally outlined by furrows which diverge forward. Alae faint. Pits small; genal caeca absent.

Remarks

Tripp *et al.* (1989) favoured the possible synonymy of *Sinoharpes* with *Dubhglasina* based on the weak development of the alae and short prolongations. Lamont's (1948b) *Dubhglasina aldonsensis* was based on a single broken, albeit well-preserved, internal mould (Figure 4 herein), referred to as "this unique and beautiful specimen" by Tripp (1976: 392). *Sinoharpes* is based on several incomplete specimens. However, both genera retain sufficient morphological features to show similarities with all species that have been referred to the Ordovician genus *Australoharpes*. The elongate glabella, wide (tr.) axial furrows, wide and flat brim, and elongate cephalon shape distinguishable in *Dubhglasina* and *Sinoharpes*, are present in *Australoharpes*. *Sinoharpes* does share two common characteristics with *Dubhglasina*, which are not present in the described species of *Australoharpes*: the uneven brim length, presence of caeca and relatively deep S1. However, these attributes do not justify the generic separation of these forms from *Australoharpes*.

Lamont (1948b) distinguished *Dubhglasina* from *Scotoharpes* "by absence of deep furrow between outer and inner parts of cheeks in front of glabella, by poorer development of alae and by absence thereon of bifurcating suture lines; also by absence of "genal caecum" running postero-laterally from eye". As these features are present in species of *Australoharpes*, and given that the name *Dubhglasina* was erected prior to *Australoharpes*, then *Australoharpes*, like *Sinoharpes*, is herein regarded as a subjective synonym of *Dubhglasina*. This extends the geographic range of *Dubhglasina* to Australia, South America and China and the stratigraphic range from the Lower Caradocian to the early Ashgill (Upper Ordovician).

Species Included

Australoharpes depressus Harrington and Leanza,

1957; *A. expansus* Jell, 1985b; *A. pospelovi* Petrunina, 1966; *A. precordilleranus* Baldis and Gonzalez, 1986; *A. singletoni* Jell, 1985b; *Sinoharpes yunnanensis* Sheng, 1974.

Dubhglasina parvula (M'Coy, 1851)
Figure 4

Harpes? parvulus M'Coy, 1851: 387; M'Coy 1852: 337, 374, pl. 1L, fig. 3; Whittington 1950a: 55; Morris 1988: 104.

Dubhglasina aldonsensis Lamont, 1948b: 533; Tripp 1976: 391–392; Přibyl and Vaněk 1986: 17.

Dubhglasina parvula (M'Coy, 1851); Owen *et al.* 1996: 136, 140, fig. 3C; Armstrong *et al.* 2000: 36.

Remarks

M'Coy (1851) described *Harpes? parvulus* from early Caradoc clasts in the Late Ordovician Wrae Limestone near Peebles, Scotland. Owen *et al.* (1996) have pointed out that this form is very similar to *Dubhglasina aldonsensis*, the only differences being the complete absence of alae (they are said to be 'just discernible' in *D. aldonsensis* (Owen *et al.* 1996: 140) and a 'slightly shorter (sag.) brim which has a more transverse posterior edge mesially' in *H? parvulus*. The cladistic analysis (Figure 5; Table 2) codes *A. aldonsensis* and *A. parvula* identically. The small 'just discernible' alae in *A. aldonsensis* is perhaps the only feature that would separate the specimens from Aldons Old Quarry Girvan from the single specimen of *A. parvula* from the Wrae Limestone of the same age. A slight difference that

exists in the transverse posterior margin is not sufficient justification to separate the two species. Moreover the question of whether or not alae are truly absent in the poorly preserved single specimen of *A. parvula* is debatable (Owen *et al.* 1996: 137, fig 3C). Following Owen *et al.* 1996, it is considered herein that *Harpes? parvula* belongs in *Dubhglasina*. Consequently, *Dubhglasina aldonsensis* is herein considered to be a junior subjective synonym of *Dubhglasina parvula*.

Cladistic analysis

Outgroups

The type species of *Brachyhipposiderus* and *Eoharpes* were used as outgroups for *Dubhglasina*. *Brachyhipposiderus* and *Eoharpes* share some similar morphological characteristics with *Dubhglasina*, such as short prolongations and a vaulted glabella and palpebral field. The data matrix with codings for all eight species is given in Table 2.

Characters

0. *Brim length (sag. vs. exsag.)*. Brim length determines the shape of the whole cephalon. State 0 indicates a 'square' shaped brim common in the outgroup as opposed to an elongate shaped brim dominant in *Dubhglasina*.

0: square shaped; 1: elongate

1. *Brim length versus glabella length (sag)*. The size of the glabella may vary in proportion to the brim sagittally. State 0 indicates a short brim, common in *Brachyhipposiderus* and *Eoharpes* and in the Harpididae. *Dubhglasina* usually has an equal to long brim.

0: short; 1: equal; 2: long

2. *Girder kink*: Measured as a slight convex 'kink' sagittally, in front of the preglabellar furrow. The 'kink' is best seen in undistorted specimens. The convex girder is absent in both outgroups.

0: absent; 1: present



Figure 4 *Dubhglasina parvula* (M'Coy, 1851). The holotype of *Dubhglasina aldonsensis* Lamont 1948b, holotype, GLA HMA5193 from the ?Middle Ordovician *Didymograptus superstes* Mudstones, Aldons Old Quarry, near Girvan, Ayrshire, Scotland, x3.5.

Table 2 Data matrix for *Dubhglasina*. '?' indicates missing data.

	0	1	2	3	4	5	6	7	8
<i>Brachyhipposiderus</i>	0	0	0	0	0	1	0	0	1
<i>Eoharpes</i>	0	0	0	0	0	0	0	0	0
<i>D. aldonsensis</i>	1	1	0	0	0	1	0	?	?
<i>D. depressus</i>	1	1	1	1	1	1	0	0	?
<i>D. expansus</i>	1	1	1	1	0	1	1	1	0
<i>D. parvula</i>	1	1	0	0	0	1	?	?	?
<i>D. singletoni</i>	0	0	1	1	0	0	1	1	1
<i>D. yunnanensis</i>	1	1	0	0	0	1	1	0	?

3. *Condition of anterior boss.* The earliest known appearance of the anterior boss occurs in *Dubhglasina*. A large predominant (bulbous) boss may expand onto the brim and reach as far as the anterior border. The anterior boss develops from the inflation of the area between two anteriorly extended axial furrows. At times only a slight inflation occurs between the extended axial furrows. The anterior boss is absent in both outgroups.

0: absent; 1: axial furrows; 2: bulbous

4. *Position of eye.* Measured as the anterior or posterior (exsag.) position of the midlength of the eye in relation to the preglabellar field. State 1 is only known in *D. depressus*, in which the eyes are clearly anteriorly positioned in relation to the preglabellar field. The presence of the posteriorly positioned eye is common in later harpetids, however its occurrence in *Dubhglasina* may indicate a derived character.

0: posterolateral; 1: anterolateral

5. *Condition of eye ridge.* The eye ridge exists between the frontal lobe of the glabella and the eye. The ridge can either be transversely or posterotransversely directed adaxially from the glabella. The eye ridge is present in *Brachyhipposiderus* and absent in *Eoharpes*.

0: absent; 1: present

6. *Posterior extent of girder.* The girder forms a ridge that is separate from posterior border and is raised as far as the prolongation tip or spine. A posteriorly extended girder is absent in both outgroups.

0: absent; 1: present

7. *Convexity of the brim.* Brim convexity varies greatly in *Dubhglasina*. The brim is strongly convex in *D. singletoni* and brim convexity is absent in *D. depressus*. Convexity is not due to short prolongations and a vaulted palpebral field, as the brim is flat or even slightly convex in *Eoharpes*. A convex brim is present in all species of *Brachyhipposiderus*.

0: flat; 1: convex

8. *Presence of spine prolongation.* The only known occurrence of a spine prolongation in *Dubhglasina* is in *D. singletoni*. Other species of *Dubhglasina* may possess one. However, it is an unusual character in the Harpetidae, with the exception of *Brachyhipposiderus*. Spines are common in the Entomaspidae, and are herein considered plesiomorphic. Spines are absent in *Eoharpes*.

0: absent; 1: present

Results and Discussion

Standard parsimony analysis yielded a single parsimonious tree (length = 14; ci 64; ri 61) (Figure

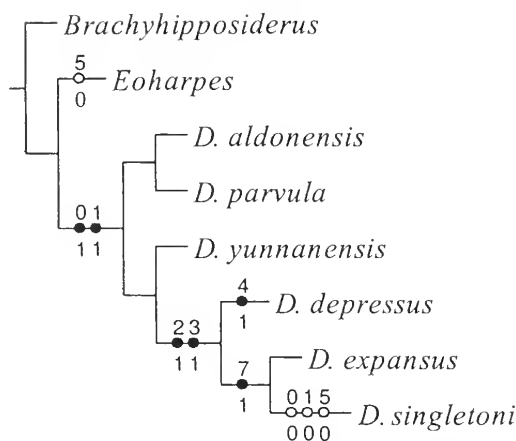


Figure 5 Standard parsimony analysis of *Dubhglasina* yielded a single most parsimonious tree (length = 14; ci 64; ri 61).

5). Three-item analysis, however, found 13 trees (length = 36; ci 69; ri 56) that formed an unresolved consensus. In the three-item cladogram *D. yunnanensis* and *D. parvula* together form a sister clade to *D. depressus*, *D. expansus* and *D. singletoni*, providing no overwhelming support for or against the synonymy of *Australoharpes* into *Dubhglasina*. The clade comprising *D. depressus*, *D. expansus* and *D. singletoni* is supported by the presence of long prolongations and a girder kink. These unique synapomorphies, however, are only present in standard parsimony analysis. The characters 'long prolongations' [8:1] and a 'girder kink' [2:1] are informative, however, they are not paramount in supporting the poorly preserved species of *Dubhglasina* that have their prolongations missing. Differences in standard parsimony and three-item analysis are difficult to assess in the *Dubhglasina* analyses due to the lack of resolution in the three-item minimal tree.

Genus *Eoharpes* Raymond, 1905 Figure 2D

Type Species

Harpes primus Barrande, 1872 from the Šárkian (Lower Ordovician) of Bohemia.

Emended Diagnosis

Cephalon semicircular, with flat brim; fringe slightly inclined anteriorly and heavily pitted with varying degrees of caeca and pitting on genal area. Genal roll steeply inclined to concave and pitted. Glabella gently convex, elongate to triangular; highest point at midline on occipital ring; L1 small, S1 posterolaterally directed, effacing adaxially. Eyes

present with eye ridge, extending to axial furrow. Alae small and depressed. Girder extending to rounded prolongation tip; prolongations short; inner margin gently concave, external rim posteriorly directed. Hypostome pear-shaped. Thorax oval, varying between twelve to fifteen segments. Small pygidium with three segments.

Remarks

Novák (1885) assigned *Harpes benignensis* Barrande, 1872 and *Harpes primus* Barrande, 1872 to *Harpina* Novák, 1884. However, the name *Harpina* was already preoccupied. Thus Raymond (1905) introduced the name *Eoharpes* into which the two Barrande species were placed. Further confusion of the generic attributes of *Eoharpes* persisted (see Sinclair (1947) and Whittington (1950a)). *Harpina rutrelum* Clarke, 1897 and *Harpina minnesotensis* Clarke, 1897, both have features characteristic of *Dolichoharpes*, even though the latter has been referred to *Eoharpes* by Přibyl and Vaněk (1986).

Eoharpes primus herschenensis (Koch and Lemke, 1996: 34, pl. 1, fig. 1) from the Ordovician of Germany, is only represented by one poorly preserved specimen. The assignment of a subspecies is not justified, with minor differences such as varying number of pits on brim and genal roll, being likely due to intraspecific variation.

Species Included

Harpes benignensis Barrande, 1872; *E. cristatus* Romano, 1975; *E. guichenensis* Henry and Phillipot, 1968; *E. macaensis* Romano and Henry, 1982.

Cladistic Analysis

Outgroups

Eoharpes and *Brachyhipposiderus* are two of the earliest known genera of harpetids. Each genus consists of primitive harpetid characteristics, such as small or absent alae, short (sag.) glabella, the presence of spines on *Brachyhipposiderus* and small subdued eyes on *Eoharpes*. Both genera do possess some apomorphic characteristics, such as absence of caecae that are common in more derived genera such as *Kielania*. *Harpides* has been selected as the outgroup for the *Eoharpes* analysis based on the aforementioned characteristics that are primitive in the Harpetidae. Rather than using the type species *Harpides hospes* Beyrich, 1846, *H. atlanticus* Billings, 1865 is coded herein, due to its excellent preservation. Coding for all character states are listed in Table 3.

Characters

0. Anterior preglabellar depression. The character can also be interpreted as the 'sagittal lengthening of the preglabellar furrow'. The anterior depression should not be confused with the steep and

Table 3 Data matrix of *Eoharpes*. '?' indicates missing data.

	0	1	2	3	4	5
<i>Harpides</i>	0	0	0	0	0	0
<i>E. benignensis</i>	1	1	1	1	0	0
<i>E. cristatus</i>	1	0	0	0	1	1
<i>E. guichenensis</i>	1	1	1	1	0	0
<i>E. macaensis</i>	0	0	0	0	1	1
<i>E. primus</i>	?	1	0	1	0	0

sometimes concave genal roll common to all known species of *Eoharpes*. The depression extends from the preglabellar furrow (sag.) and effaces posterior to the genal roll. An anterior preglabellar depression is absent in the outgroup.

0: absent; 1: present

1. Condition of eye ridge. The presence of an eye ridge is autapomorphic to all known species of *Eoharpes*. However, the ridge is diffuse in some species and distinct in others. The character is not dependent on the amount of ornament on the genal area. A diffuse eye ridge is possibly derived from a prominent ridge present in the outgroup.

0: prominent; 1: diffuse

2. Glabella shape. Two distinct glabella types exist in *Eoharpes*, the more common and plesiomorphic is an elongate shape present in the outgroup, and the derived type is triangular in shape, as displayed in *E. benignensis* and *E. guichenensis*.

0: elongate; 1: triangular

3. Inner fringe convexity. Measured as the height between the posterior border (exsag.) and the inner margin of the fringe (exsag.) in lateral view. An inflated genal area is higher than the posterior border. The outgroup lacks genal inflation and is herein considered plesiomorphic.

0: absent; 1: present

4. Condition of axial furrow posteriorly. The posterior-most part of the axial furrow opposite L1 effaces in several species of *Eoharpes*. The absence of the lateral furrow does not affect L1 size or shape. The outgroup does not display this state.

0: absent; 1: present

5. Alar size versus L1 size: Alar size is best measured against L1 as both structures are adjacent and may vary allometrically during ontogeny. Although no ontogenetic material of *Eoharpes* exists, comparable evidence can be drawn from *Dolichoharpes*. The outgroup *Harpides* and other harpidids and entomaspidids do not have developed alae. Thus small alae are herein considered plesiomorphic in *Eoharpes*.

Results and Discussion

The same single parsimonious cladogram was yielded by both standard parsimony (length = 7, ci 85, ri 87) and three-item analysis (length = 14, ci 85, ri 83) (Figure 6). *Eoharpes cristatus* and *E. macaoensis* form a clade supported by the presence of an inner marginal fringe and a posteriorly effaced axial furrow. Sisters to these are remaining *Eoharpes* species, distinguished by the presence of an anterior preglabellar depression and triangular glabella. *E. benignensis* and *E. guichenensis* are distinguished by the presence of a diffuse eye ridge. The results in the *Eoharpes* analysis are similar to those presented in the *Dubhglasina* discussion. Both genera contain two clades each that are supported by two character-states. These character-states do not represent a separate monophyletic grouping that would justify a new taxonomic group in either genus.

The monophyly of *Eoharpes* is not clear as there are no basal characters supporting the genus in either analysis. This is due to the small number of characters used in the analysis. The cladistic analysis of *Eoharpes*, however, is beneficial because it finds the relationships within the highly stratigraphically constrained group. All species occur within the Llanvirn-Llandelio (Middle Ordovician), with the exception of the poorly known *E. macaoensis*, which has a possible lower Caradoc? range (Romano and Henry 1982).

The close similarities between *E. primus*, *E. benignensis* and *E. guichenensis* were noted previously by Chavel and Henry (1966), Henry and Phillipot (1968) and Romano and Henry (1982), as similar characters within the cladistic analysis [1: 1], [2: 1] and [3: 1].

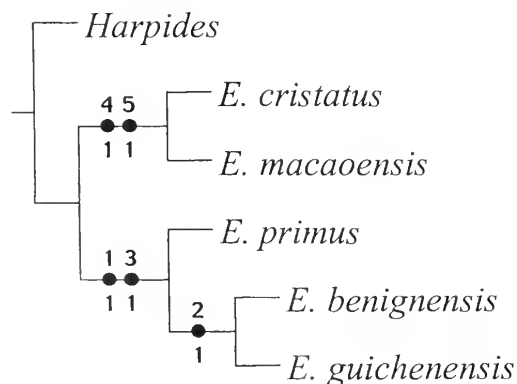


Figure 6 Standard parsimony and three-item analysis of *Eoharpes* yielded a single cladogram.

Genus *Harpes* Goldfuss, 1839

Figure 2E, F

Reticuloharpes Vaněk, 1963: 229.

Helioharpes Přibyl and Vaněk, 1981: 188–9.

Type Species

Harpes macrocephalus Goldfuss, 1839, Eifelian (Middle Devonian), Germany.

Emended Diagnosis

Cephalon semicircular to ovate. Brim flat, pitted, rim wide and raised along whole margin. Glabella elongate to sub-triangular, inflated and tuberculate. Genal roll long (sag.), convex and vaulted. Eyes set adaxially and anterior to preglabellar furrow; eye ridges weak. Alae transversely elongate, larger than L1. Thorax up to 29 segments.

Remarks

The type species of *Reticuloharpes*, *R. reticulatus*, was figured by Vaněk (1963: 228, fig. 4). The drawing, however, has several flaws. The elongate prolongations are illustrated as being longer than the cephalic length (sag.) (see characters 17 and 18 below). They are also depicted as curving adaxially to form an inwardly concave section at the base of the prolongation. Neither of these characters are present in actual specimens of *Reticuloharpes*. When measured, the prolongations are always shorter than the whole cephalic length, not longer as illustrated by Vaněk (1963: 229, fig. 4). The concave margin also does not exist on any known species of harpetid. The inward concavity is an optical illusion or 'space curve' that forms when the prolongations (that are inverted perpendicularly to the brim) are seen stereoscopically. A photograph does not capture a space curve, thus the inward concavity is absent.

Other diagnostic features of *Reticuloharpes* including a vaulted glabella 'narrowing towards the frontal part, with a median elevation' (Vaněk 1963: 229), are characteristic of all *Harpes*, *Reticuloharpes* and *Helioharpes* species. Vaněk (1963) noted that "the nearest genus may be *Harpes*", however it differs by the "finer brim perforation and...single row of distinct perforations at the external rim" and the shape and size of the eye ridges. These characters distinguish the characteristics (homologues) that are variable between different species of the same genus rather than the taxonomic variations between two different genera.

A similar criticism can be made of *Helioharpes* Přibyl and Vaněk (1981). The diagnostic characters are similar to the *Harpes* diagnosis of Whittington (1959). The distinguishing characters of *Helioharpes*, namely the sunken alae and irregular radial ridges on the brim and conical glabella as present in *H. perradiatus* Richter and Richter, 1943 and *Helioharpes*

radians Richter, 1963 and *H. transiens* Barrande, 1872, are also diagnostic of *Harpes*. Consequently, *Reticuloharpes* and *Helioharpes* are herein considered to be subjective junior synonyms of *Harpes*.

Species Included

H. dvorcensis Prantl and Přibyl, 1954; *H. escoti* Bergeron, 1887; *H. fornicatus* Novák, 1890; *H. forojuliensis* Gortani, 1909; *H. koeneni* Wedekind, 1914; *H. nymageensis* Fletcher, 1975; *H. ormistoni* Přibyl and Vaněk, 1986; *H. perradiatus* Richter and Richter, 1943; *H. polaris* Maksimova, 1977; *H. pyrenaicus* Barrios, 1886; *H. radians* Richter, 1963; *H. reticulatus* Hawle and Corda, 1847; *H. rouvillei* Frech, 1887; *H. transiens* Barrande, 1872; *H. whidbournei* Whittington, 1950a; *H. sp. nov.* (Feist 1977); *H. sp. nov.* (Feist 1977); *H. sp.* (Ormiston 1971); *H. sp.* (Holzapfel 1895); *H. sp.* (Chlupáč 1969); *H. sp.* (Weber 1932).

Cladistic analysis

Outgroups

The type species of *Eoharpes*, *Bohemoharpes* and *Lioharpes*, have been chosen as outgroups for the *Harpes* analysis. *Bohemoharpes* and *Lioharpes* exhibit significant characteristics atypical of *Harpes*, such as the large alae, wide (tr.) and vaulted glabella, prominent genal roll and wide brim (sag.). The Middle Devonian *Harpes* occurs in younger strata than *Bohemoharpes* and is contemporary with *Lioharpes*.

Many problematic species have been assigned to *Harpes* and left there during the many revisions by Prantl, Přibyl and Vaněk. Due this practice, the monophyly of *Harpes* may be questioned on the basis of the addition of species with plesiomorphic characteristics commonly attributed to *Eoharpes*. Therefore, *Eoharpes* has been added to polarize any primitive characteristics in *Harpes* to test the monophyly of the genus. *H. koeneni* and *H. dvorcensis* are based on several poor fragmentary crania and have been omitted from the analysis. The character state data matrix is listed in Table 4.

Characters

0. *Brim shape - elongate*. The shape of the brim is influenced by the different conditions of the brim and prolongations. An elongate brim is typically longer (sag.) than it is wide (tr.). The elongate brim is present in *Lioharpes*.

0: absent; 1: present

1. *Cephalon shape - semicircular*. The semicircular cephalon is typically wider (tr.) than it is long (sag.). Prolongation length does not influence the shape of the cephalon. *Eoharpes* is semicircular.

0: absent; 1: present

Table 4 Data matrix for *Harpes*. '?' indicates missing data

	0	1	2	3	4	5	6	7	8	9	1	1	1	1	1	1	1	1	1
											0	1	2	3	4	5	6	7	8
<i>Eoharpes</i>	0	1	0	0	0	1	1	0	0	0	1	0	1	1	0	1	0	0	1
<i>Bohemoharpes</i>	0	0	0	1	0	1	0	1	0	0	1	0	1	0	?	?	?	0	1
<i>Lioharpes</i>	1	0	1	1	0	0	1	1	1	1	0	0	1	0	0	0	1	0	1
<i>H. perradiatus</i>	1	0	0	0	1	1	1	1	0	0	1	0	1	0	1	1	1	1	0
<i>H. radians</i>	0	1	0	1	1	1	0	1	0	?	?	?	?	?	?	?	?	1	1
<i>H. transiens</i>	0	1	0	1	0	1	1	0	1	0	0	0	1	0	?	?	?	1	1
<i>H. frechi</i>	1	0	0	1	0	1	1	0	1	0	0	0	1	0	1	1	0	1	1
<i>H. intertextus</i>	1	0	0	1	0	1	1	1	0	1	0	0	1	1	1	1	1	?	?
<i>H. latilimbatus</i>	?	?	?	1	0	0	1	1	0	1	1	0	0	0	0	1	0	?	?
<i>H. macrocephalus</i>	0	1	1	1	0	1	0	1	0	1	0	0	1	1	1	0	1	0	1
<i>H. ormistoni</i>	0	1	1	1	0	1	1	1	0	1	0	0	1	0	0	1	0	0	1
<i>H. polaris</i>	0	1	1	1	0	0	1	1	0	1	0	1	1	?	?	?	1	0	0
<i>H. rouvillei</i>	?	?	?	1	0	0	1	1	0	1	0	0	1	1	1	1	0	?	?
<i>H. whidbournei</i>	1	0	1	1	0	1	1	?	0	?	?	0	0	0	?	0	1	0	0
<i>H. escoti</i>	0	1	1	1	0	1	0	1	1	0	0	0	1	1	0	1	0	0	1
<i>H. nymageensis</i>	0	1	0	?	0	1	0	1	0	?	?	0	?	?	?	?	1	0	0
<i>H. reticulatus</i>	1	0	1	1	0	1	0	1	0	0	0	1	1	0	1	0	0	0	1
<i>H. socialis</i>	0	1	0	1	0	1	0	0	0	1	0	0	1	0	1	1	0	0	1

2. *Cephalon shape - pentagonal*. The pentagonal shape is influenced by a long brim (sag.), widening (tr.) anteriorly. A pentagonal cephalon is typically wider anteriorly than posteriorly. A cephalon that is wider (tr.) than it is long (sag.) and has an anteriorly expanding cephalon is coded as 0: 0, 1: 1, 2: 1. The pentagonal cephalic shape is absent from all outgroups.

0: absent; 1: present

3. *Anterior boss*. There are several states that indicate a developing boss. These are an extension of the axial furrows onto the genal roll and the inflation of the genal roll (sag.) in front of the preglabellar furrow. The anterior boss is present in both *Bohemoharpes* and *Lioharpes*, but absent in *Eoharpes*.

0: absent; 1: present

4. *Conical frontal lobe*. The conical frontal lobe is a separate structure to the anterior boss. The conical lobe is an extension of the glabella onto the genal roll. In several specimens the lobe may expand anteriorly as in *Helioharpes radians*. This condition may be present with an anterior boss or sagittal crest (see character 8). The conical lobe is unique to *Harpes*.

0: absent; 1: present

5. *Glabella shape - elongate*. There are several shapes of the glabella, some unique to one species. All shapes, however, conform to one of two conditions, elongate or triangular. The combination of these two characters yields a bullet shape. An elongate glabella has a relatively consistent length and is

longer (sag.) than it is wide (tr.). Elongated glabella condition is present in *Bohemoharpes*.

0: absent; 1: present

6. *Glabellar shape - sub-triangular*. A sub-triangular glabella lacks parallel axial furrows. The glabella is of varying length (sag.), widest (tr.) in the posterior or mid region (anterior to the alae) of the glabella. The sub-triangular glabella is present in *Lioharpes*. The long triangular shaped glabella is typical of *Helioharpes transiens*, *Harpes intertextus* and *Eoharpes* and is coded as 5: 1, 6: 1.

0: absent; 1: present

7. *Girder kink*. See character 2 in the *Bohemoharpes* analysis. The kink is found in *Bohemoharpes* and *Lioharpes*, but is absent in *Eoharpes*.

0: absent; 1: present

8. *Sagittal crest*. The sagittal crest occurs on the whole glabellar midline (sag.) and effaces posteriorly. The crest is absent on the preglabellar furrow and the occipital ring. The crest is present in *Lioharpes* and other genera with vaulted glabellae.

0: absent; 1: present

9. *Preglabellar transverse ridge*. The preglabellar furrow is deeper in the presence of vaulted ridges. The transverse glabellar ridge is present in *Lioharpes*.

0: absent; 1: present

10. *Lateral position of eye*. Measured as the lateral position of the midlength of the eye in relation to the abaxial extent of the alar furrow. A score of 10: 1 would indicate that the eye is closer to the axial furrow than the most lateral extent of the alar furrow (positioned closer to the inner margin than to the axial furrow). The position of the eye varies between species of the outgroup, however the type species of *Eoharpes* and *Bohemoharpes* commonly have the eye positioned abaxially from the alar furrow.

0: eye closer to alar furrow; 1: eye closer to axial furrow

11. *Anterolateral position of eye (exsag.)*. Measured as the position of the midlength of the eye in relation to the preglabellar furrow. The score 11: 1 would indicate that the eye is situated laterally to the preglabellar furrow. The state 11: 1 is rare and does not occur in any of the type species.

0: eye situated away from preglabellar furrow; 1: eye situated laterally to preglabellar furrow

12. *Alar size*. The size of the alae are measured in proportion to L1, not in proportion to the genal area. The state 12: 1 would indicate that the alae are larger than L1. In the case of vaulted alae, the posterior extent axial furrow is used to distinguish

between both organs. Small alae are absent in the outgroup.

0: smaller than L1; 1: larger than L1.

13. *Condition of the alar furrow*. The alar furrow may be continuous with the posterior border furrow. This condition forms a wide furrow (tr.) between the ala and posterior border furrow. The alar furrow is continuous with the posterior border furrow in *Lioharpes* and *Bohemoharpes*.

0: absent; 1: present

14. *Sagittal node*. The sagittal node occurs on the anterior part of L0. The sagittal node is absent in *Lioharpes* and *Eoharpes*.

0: absent; 1: present

15. *Length of L0 (sag.) - long*. There are three distinct conditions of L0. It is either longer [15: 1], narrower [16: 1] or the same length [15: 1, 16: 1] as S0 (sag.). A long L0 is common in *Lioharpes* and *Eoharpes*.

0: not longer than S0; 1: longer than S0

16. *Length of L0 (sag.) - narrow*. A narrow L0 can be associated with a narrow S0. However a score of 16: 1 indicates that L0 is relatively narrower than S0.

0: L0 not narrow; 1: L0 narrow

17. *Prolongation longer (exsag.) than cephalic length (sag.)*. Prolongation length is measured from the base (opposite the posterior border furrow) to the tip. Posterolaterally directed spines are measured as the distance along the external rim. The cephalic length (sag.) is measured from the posterior margin of L0 (sag.) to the anterior border (sag.). Spine length is short in all outgroups.

0: shorter; 1: longer

18. *Prolongation narrower (exsag.) than prolongation length (sag.)*. See description above (Character 17).

0: shorter; 1: longer

Results and Discussion

Standard parsimony analysis yielded a completely unresolved consensus tree of 50 trees (length=46, ci 41, ri 57). Three-item analysis found one minimal tree (length = 653, ci 73, ri 63) (Figure 7), in which species of *Helioharpes* and *Reticuloharpes* are scattered throughout *Harpes*. The basal autapomorphies include the presence of a semicircular shaped brim [1:1], long prolongations [17:1] and eyes situated laterally to the preglabellar furrow [11:1]. There are no basal autapomorphies that define *Harpes*.

The genus *Harpes* contains poorly known species that exhibit general characteristics of the Harpetidae, namely the vaulted cranium, inflated glabella and wide perforated brim. Unfortunately *Harpes* has been used as a taxonomic dumping ground from which better known species have been

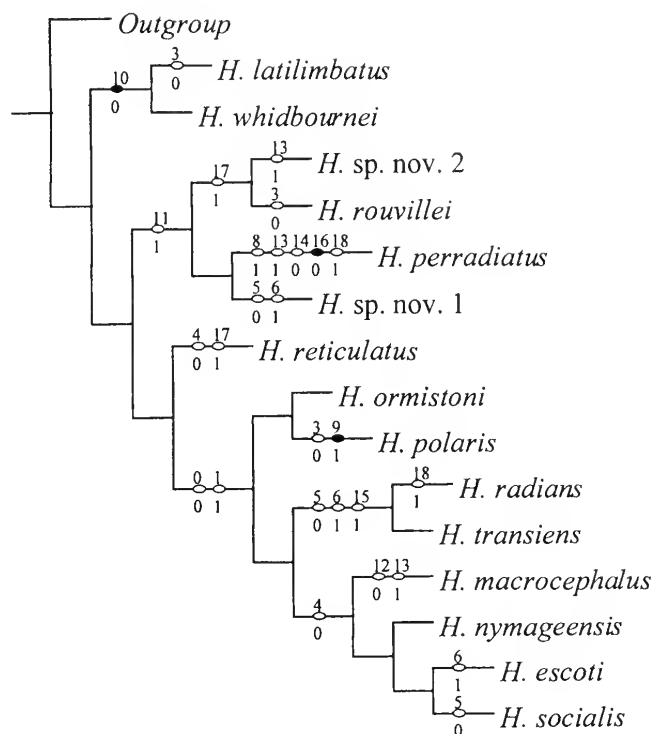


Figure 7 Three-item analysis of *Harpes* yielded a single minimal tree (length = 653, ci 73, ri 63).

retrieved to form new genera based only on the characteristics that distinguish them as species, *sensu* Vaněk (1963) and Příbyl and Vaněk (1981). *Harpes*, however, has been non-monophyletic since its erection by Goldfuss (1839). At present species of *Scotoharpes*, *Bohemoharpes*, *Kielania* and *Hibbertia* all have been diagnosed as *Harpes* at some point. Whether any new genera lie within *Harpes* is difficult to surmise. *Harpes* monophyly can only be supported or falsified once new and better specimens and characters are discovered, and a new cladistic analysis performed.

Genus *Hibbertia* Jones and Woodward, 1898

Figure 2I

Metaharpes Lamont, 1948a.

Platyharpes Whittington, 1950a: 10; Whittington 1950b: 302.

Paraharpes Whittington, 1950a: 11, Dean 1971: 9; Owen 1981: 32; Owen and Clarkson 1992: 11.

Harpesoides Koroleva, 1978: 216; Příbyl and Vaněk 1986: 24.

Wegelinia Příbyl and Vaněk, 1981: 190.

Thorslundops Příbyl and Vaněk, 1981: 190.

Type species

By monotypy, *Harpes flanaganii* Portlock, 1843=*Hibbertia orbicularis* Jones and Woodward, 1898 from the Caradoc Bardahessiagh Formation of Pomeroy County, Tryone, Northern Ireland.

Emended Diagnosis

Cephalon semicircular to ovate in outline; brim either flat to concave or strongly convex. Genal roll wide (tr.); transverse preglabellar ridge continuous with eye ridges when present. Glabella strongly vaulted, bullet shaped and lacking ornament. Eyes adaxial to alae; eye ridges present, posterior ocular line effacing on genal roll. L1 triangular shaped; L0 deep and long (sag.), at times continuous with S0. Alae larger than L1 and vaulted, rising steeply toward glabella. Alae ovate, anteriorly directed. Interlar furrow (Figure 1) present. Anterior alar ridge high when present. Coarse pitting on extremities of brim to covering entire brim; large pits on genal area opposite alae. Caeca rare on brim, confined to genal area. Hypostome subquadrangular; anterior wings large. Thorax between 10-25 segments; pygidium small with 5-6 segments.

Remarks

Whittington (1950a: 11) noted the close relationship between *Paraharpes* and *Platyharpes*, but did not refer to any strong similarities between *Hibbertia* and *Paraharpes*. There were no further mentions of any similarities between *Hibbertia* and *Paraharpes* in Whittington's (1950b) discussion of the synonymy of *Platyharpes* and *Paraharpes*. A later re-diagnosis of *Hibbertia* (Whittington 1959: 418) highlighted the differences from *Paraharpes*, notably the subcircular outline of the cephalon, narrower genal roll, broader brim, smaller pits on fringe and thorax with fewer than 10 segments. Dean (1971: 5) suggested that both the position of the girder and its extension to the tips of the prolongations are features that distinguish *Paraharpes* from *Hibbertia*.

Owen (1981), however, noted only a slight distinction between the genera, highlighting that each diagnosis can "effectively be applied to the type species [*Hibbertia flanaganii*]" (Owen 1981: 32). Owen (1981) synonymized *Metaharpes* Lamont, 1948b with *Hibbertia* (see Armstrong 2000), and *Harpesoides* Koroleva (1978) with *Paraharpes*. Přibyl and Vaněk's (1986) diagnosis of *Paraharpes* points out its close similarity to *Hibbertia*, differing only "in the oval outline of the cephalon, broader genal roll... narrower flat brim with rather large pits and great number of thoracic segments" (Přibyl and Vaněk 1986: 24), echoing Whittington (1959). Owen and Clarkson (1992) noted that the diagnostic differences between the two genera, as stated by Přibyl and Vaněk (1986), were 'very variable, non-diagnostic characters' and synonymized *Paraharpes* with *Hibbertia* (Owen and Clarkson 1982: 11), a move that was endorsed by Lespérance and Weissenberger (1998: 307–308).

In addition to the above synonymies, the two genera *Wegelinia* and *Thorshundops* may also be synonymized with *Hibbertia*. Both genera contain one species each, *Harpes wegelinei* Angelin, 1854 and *H. dalecarlicus* Thorslund, 1930 respectively. *Wegelinia* was based on a strongly convex brim and lack of functional organs (Přibyl and Vaněk 1981). *Thorshundops* was based on smaller eye tubercles and a slightly wider brim and narrower prolongations (Přibyl and Vaněk 1981). The diagnoses of both genera do not differ from that of *Hibbertia*. Consequently, *Wegelinia* and *Thorshundops* are herein considered to be junior subjective synonyms of *Hibbertia*.

Species Included

Metaharpes amibouei Lamont, 1948b; *Harpes anticostiensis* Twenhofel, 1928; *H. balclatchiensis* Whittington, 1950a; *Hibbertia conistonensis* Lespérance and Weissenberger, 1998 [= *Paraharpes whittingtoni* McNamara, 1979]; *Harpes costatus* Angelin, 1854; *H. dalecarlicus* Thorslund, 1930; *H. (Eoharpes) hornei* Reed, 1914; *Paraharpes inghami*

Owen, 1981; *Harpesoides* (?) *karamolensis* Koroleva, 1978; *H. (?) necopinus* Koroleva, 1978; *Harpes ottawaensis* Billings, 1865; *Eoharpes perceensis* Kindle, 1945; *Paraharpes ruddyi* Whittington, 1950a; *Harpes similis* Nikolaisen, 1965; *Paraharpes trippi* Whittington, 1950a; *Harpes valcourensis* Shaw, 1968; *H. wegelinei* Angelin, 1854; *H. whittingtoni* Tripp, 1965; *H. (?)* sp. (Schmidt 1894); *H. (?)* sp. (Wiman 1908); *H. (?)* sp. (Shaw 1968); *H. (?)* sp. (Bolton 1981); *H. (?)* sp. (Tripp 1976); *H. (?)* sp. (Tripp 1979).

Cladistic analysis

Outgroup

The type species *Eoharpes prinus* and *Dubhglasina depressus* have been chosen as outgroups for the *Hibbertia* analysis. The outgroups lack the well developed alae, anterior boss, convex brim and long prolongations, but do possess the wide brim, particularly in *Dubhglasina*, short glabella (sag.), long (tr.) S0, vaulted genal field and genal roll, flat brim and coarse pitting.

Hibbertia karamolensis and *H. necopinus* Koroleva (1978) are described from broken brim and cephalic material. Both are difficult to recognise as species of *Hibbertia* and are in need of revision. Coding these species is not possible and they are excluded from the analysis. Character states are listed in Table 5.

Characters

0. *Brim concavity (sag.)*. Brim concavity is measured sagittally anterior to the genal roll. Flat brims with raised rims may be confused as being concave and should be coded as state 0.
0: absent; 1: present

Table 5 Data matrix for *Hibbertia*. '?' indicates missing data.

	0	1	2	3	4	5	6	7	8	9	1	1	1	1	1
											0	1	2	3	
<i>Eoharpes</i>	0	0	0	0	0	1	?	0	?	0	0	0	0	0	0
<i>Dubhglasina</i>	0	0	2	0	0	1	?	0	?	0	0	0	0	0	0
<i>H. balclatchiensis</i>	1	0	0	0	0	0	0	1	0	1	0	1	0	1	1
<i>H. conistonensis</i>	1	0	?	?	?	0	?	1	0	1	0	1	0	1	1
<i>H. costatus</i>	0	1	1	0	1	0	1	1	1	0	0	0	0	0	0
<i>H. dalecarlicus</i>	?	0	2	?	?	0	?	?	1	0	1	0	1	1	0
<i>H. hornei</i>	0	0	1	1	0	0	0	0	?	1	1	0	2		
<i>H. inghami</i>	1	0	2	1	1	0	0	1	0	1	0	1	0	1	0
<i>H. orbicularis</i>	1	1	0	0	1	0	0	1	1	1	0	1	0	1	0
<i>H. ottawaensis</i>	0	1	1	0	1	0	0	1	1	1	1	1	1	1	1
<i>H. perceensis</i>	?	0	0	0	1	0	?	1	0	1	0	1	0	1	1
<i>H. similis</i>	1	0	1	?	?	0	0	0	?	?	1	0	1	1	1
<i>H. trippi</i>	1	0	0	0	1	0	0	1	0	1	0	1	0	1	0
<i>H. valcourensis</i>	1	0	0	0	1	1	1	?	?	1	0	1	?		
<i>H. wegelinei</i>	0	1	0	1	1	0	0	1	0	?	?	0	1	0	?
<i>H. whittingtoni</i>	1	1	0	0	?	0	?	?	?	?	?	1	?	1	?

1. *Brim convexity (sag.)*. Both brim concavity and convexity can occur at the same time, depending on the convexity of the glabella and genal roll. Brim convexity is measured sagittally anterior to the genal roll.

0: absent; 1: present

2. *Anterior boss (sag.)*. The presence of either a ridge extending from the frontal lobe of the glabella to the girder or a large bulbous anterior boss extending at times to the anterior border are different states of character 2. Both these states are derivatives of the extension of the axial furrow pair into the genal roll. The two axial furrows either increase in depth, creating a ridge (2: 1), or curve abaxially to form a boss.

0: absent; 1: furrow pair or distinct ridge; 2: boss

3. *Anterior glabellar depression*. This may be mistaken for a long (sag.) prelabellar furrow. However, it can be found in association with a transverse prelabellar ridge (see character 4).

0: absent; 1: present

4. *Presence of prelabellar transverse ridge*. The ridge is situated between the prelabellar furrow and the girder, and is parallel to the prelabellar furrow between the eye ridges. In several cases the ridge may be continuous with the eye ridges, but there may be little relationship between either homology.

0: absent; 1: present.

5. *Position of eye (exsag.)*. Measured as the abaxial extremity of the eye in relation to the most abaxial extent (tr.) of the ala.

0: adaxial; 1: abaxial

6. *Direction of eye ridge*. Only two states occur in *Hibbertia*. Transversely directed eye ridges may occur early in ontogeny, however fully developed forms possess either state 0 or 1.

0: anterolaterally directed; 1: posterolaterally directed

7. *Presence of ocular furrow*. The ocular furrow is situated posteriorly to the eye and may be continuous with the axial furrow and efface abaxially to the eye ridge.

0: absent; 1: present

8. *Condition of interalar furrow*. The interalar furrow is parallel and abaxial to the axial furrow. All species of *Hibbertia* share this character and the two states are prominent. The course of the interalar furrow is consistently parallel to the axial furrows, although in [8: 1] the furrows are adaxial posteriorly and intersect the axial furrows opposite L1.

0: continuous with posterior border furrows; 1: continuous with axial furrows.

9. *Anterior alar ridge*. The alar ridge is situated between an adaxial extension of the palpebral furrow that is continuous with the axial furrow and the anterior extent of the alar furrow. The ridge is parallel to the alar furrow, below the eye to the intersection of the eye ridge and the axial furrow.

0: absent; 1: present

10. *Coarse pitting and caeca on brim*. Coarse pitting and caeca together serve as a possible homologous organ to that of a functional brim. Fine pits or granules have not been associated with a functional brim and herein are treated as an unrelated homology.

0: absent; 1: present

11. *Caeca on genal area*. Caeca and pit structures independent as primary homologies and are inter-dependant. Caeca present on genal area below the eye and opposite alae are coded as state 1.

0: absent; 1: present

12. *Coarse pits on genal area*. The presence of coarse pits below eye and opposite alae are coded as state 1. Several species may possess a cluster of coarse pits below the eye.

0: absent; 1: present

13. *Prolongation length (exsag.) versus cephalic length (sag.)*. Prolongation length is measured from the mid-point of S0 to the most posterior extent of the prolongation spine/tip against cephalic length. Accurate length of the spine is difficult to measure in ovate or circular brims with adaxially directed tips or spines.

0: less; 1: equal, 2: more

Results and discussion

Standard parsimony analysis resulted in a consensus of 8 trees (length = 33, ci 48, ri 61) (characters mapped on to first tree Figure 8) with 6 nodes, one of which is a polytomy of nine taxa (Figure 9). Topologically the consensus provides minimal support for *H. wegelini*, *H. costatus* and *H. hornei* [2: 1], a clade basal to *H. dalecarlicus* and *H. inghami*. Three-item analysis yielded a minimal tree of 16 most parsimonious trees (length = 842, ci 70, ri 57) (Figure 10). The minimal tree consists of eight nodes, two of which are polytomies that provide little information regarding relationships of taxa. *H. costatus* and *H. wegelini* are sister taxa within the polytomy and reinforce the synonymy of *Wegelinia* and *Thorslundops* within *Hibbertia*. *Hibbertia conistonensis* and *H. balclatchiensis* form a sister clade to *H. perceensis*, *H. ottawaensis*, *H. orbicularis* and *H. whittingtoni*.

The three-item and standard parsimony analyses vary greatly in topology, but do contain some similarities. Both analyses, for instance, support the Swedish group of *H. wegelini* and *H. costatus* and a

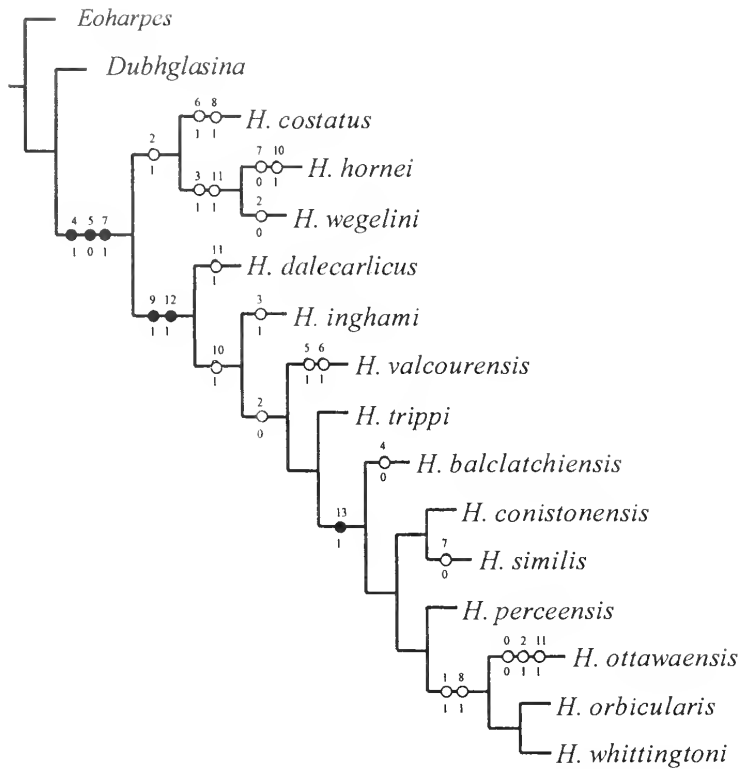


Figure 8 Standard parsimony analysis of *Hibbertia*. Characters mapped onto first tree from 33 most parsimonious trees (length = 33, ci 48, ri 61).

monophyletic *Hibbertia*, consisting of taxa formerly assigned to *Platyharpes*, *Paraharpes*, *Wegelinia*, *Thorslundops* and *Metaharpes*. The standard parsimony analysis contains a clade consisting of *H. costatus*, *H. hornei* and *H. wegelini* based on the presence of an extended axial furrow pair on the prelabellar field that is absent in the three-item analysis. The standard parsimony and three-item analyses share similar character-states to support the monophyly of *Hibbertia* [4: 1, 5: 0, 7: 1]. In the three-item analysis, however, it is interesting to note that *Hibbertia* is supported by one extra character-state, namely the presence of an anterior alar ridge that only appears later to support the unresolved clade containing a large portion of the *Hibbertia* species, with the exception of the aforementioned *H. costatus*, *H. hornei* and *H. wegelini* clade. Differences in the basal node configuration are a result of the implementation of two conceptually different methods.

Genus *Kielania* Vaněk, 1963

Kielania (*Lowtheria*) Prantl and Příbyl, 1981: 189.

Type Species

Harpes waageni Prantl and Příbyl, 1954 from the

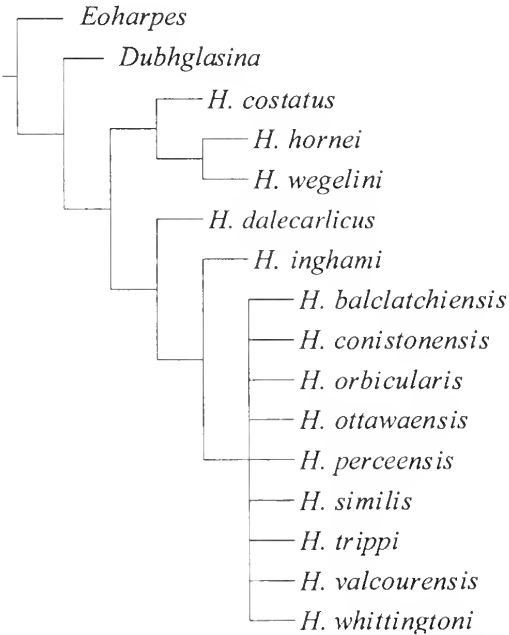


Figure 9 Standard parsimony analysis of *Hibbertia* found a consensus of 33 most parsimonious trees.

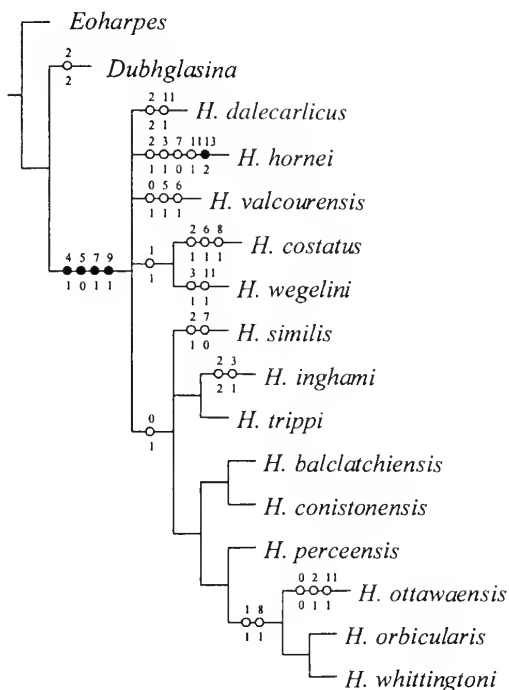


Figure 10 Three-item analysis of *Hibbertia* found a minimal tree from 16 trees (length = 842, ci 70, ri 57).

Lower Devonian (Pragian) Dvorce-Prokop Limestone, Prague, Czech Republic.

Emended Diagnosis

Semi-circular cephalon with vaulted brim. Ovoid glabella with median tubercle (sag.) on frontal lobe. Prolongations short and alae small. Hypostome with convex anterior margin and small posterior wings. Thorax with up to 16 segments; pygidium wide, with 4–6 axial rings.

Remarks

Příbyl and Vaněk (1986) erected the subgenus *Kielania* (*Lowtheria*), on the basis of one species, *K. (L.) triabsidata*. The formalisation of *K. (Lowtheria)* is based purely on diagnostics of a single species rather than a distinct group and is herein synonymised as *Kielania*.

Ebach and McNamara (in prep.) are describing four new species of *Kielania* from latest Frasnian sediments associated with extensive reef deposits in the Canning Basin in Western Australia. The descriptions of the new species and a new genus will be accompanied by a cladistic analysis.

Genus *Lioharpes* Whittington, 1950a

Figure 2B

Fritchaspis Vaněk, 1963: 227–8; Příbyl and Vaněk 1986: 20–1.

Type Species

Harpes venulosus Hawle and Corda, 1847, from the Pragian of Bohemia.

Diagnosis

Cephalon semicircular; alae large, smooth with deep alar furrows. Caeca and pits well developed on brim and genae. Hypostome pear-shaped with broad, acute anterior wings and narrow lateral borders.

Remarks

Fritchaspis was erected by Vaněk (1963: 227–8) who considered that it was a direct descendant of *Lioharpes*, differing in the “more dense and finer perforations” on the brim and preglabellar field, and by a less convex preglabellar field and rounder shape of the frontal lobe, the indistinct eye ridges and in that the “general arch of the cephalon is much smaller”. None of the above features can be distinguished as individual characters. Characters such as a less convex preglabellar field and rounder shape of the frontal lobe are variations that are present between species, rather than taxonomic distinctions between two subgenera. The diagnosis of *Fritchaspis* is synonymous with that of Whittington’s (1950a) diagnosis of *Lioharpes*. Consequently, *Fritchaspis* is considered to be a subjective junior synonym of *Lioharpes*.

Vaněk (1963) gave no reason as to why he considered *Fritchaspis* to be a direct descendant of *Lioharpes*, other than stating that it “shows the nearest relations to *Lioharpes*”. A later revision of *Lioharpes* treats *Fritchaspis* as a subgenus of *Lioharpes*, “that gave rise to the nominate subgenus *Lioharpes* (*Lioharpes*)” (Příbyl and Vaněk 1986: 9). The change of both the status and relationship of *Lioharpes* (*Fritchaspis*) is possibly due to the assignment of existing species into *Fritchaspis* which is positioned lower in the stratigraphic record.

Lioharpes venulosus (Hawle and Corda, 1847)

Harpes ruderalis Hawle and Corda, 1847: 165. nov. emend. Prantl and Příbyl 1954: 140.

Lioharpes (*Lioharpes*) *venulosus* alter Příbyl and Vaněk, 1986: 30.

Lioharpes klukovicensis Vaněk, Vokáč and Hörbinger, 1992: 99.

Discussion

The differences between the single specimen of *L.*

klukovicensis and other species of *Lioharpes* are the "distinctly ovoid glabella lacking carina.... concave brim...pronounced radiating ridges at the genal roll/brim boundary, flat brim and clearly wider glabella at its posterior margin" (Vaněk *et al.* 1992: 99). This diagnosis is consistent with figured specimens of *L. venulosus*, with the exception of the ovoid glabella that is absent in the specimen of *L. klukovicensis* (Vaněk *et al.* 1992, pl. 2, fig. 1). Prantl and Přibyl (1954) resurrected *L. ruderalis*, synonymized into *L. venulosus* by Hawle and Corda (1847), citing a wider cephalon (tr.), cylindrical glabella, fine perforations on brim and the position of the eyes. However, a wider brim is common in slightly deformed specimens, and finer perforations are apparent in external moulds rather than internal moulds. *Lioharpes venulosus* is perhaps the most common harpetid in the Lochkov Limestones of Bohemia, where most harpetids are found. Morphological variations and deformations used to diagnose *L. ruderalis* above are common in most specimens of *L. venulosus*.

***Lioharpes montagnei* (Hawle and Corda, 1847)**

Harpes montagnei Hawle and Corda, 1847: 165.

Harpes perneri Prantl and Přibyl, 1954: 149.

Discussion

Prantl and Přibyl (1954) believed *Kielania dorbignyana* (Barrande, 1846) to most closely resemble *L. perneri*, differing only by the smaller eyes, a raised rim, wider alae (tr.) and finer perforations on the cheek-roll and brim. Prantl and Přibyl (1954: 150) suggested that *Lioharpes perneri* closely resembles *Kielania convexus* (Hawle and Corda, 1847) and *K. novaki* Prantl and Přibyl (1954), more so than any species of *Lioharpes*. The bulbous anterior boss present on the genal roll, long brim (sag.) and strongly tapering prolongations in *L. perneri*, features absent in *K. dorbignyana* are, however, all characteristic of *L. montagnei*. *Harpes pernei* is herein considered to be a subjective junior synonym of *L. montagnei*.

Species included

Harpes altaicus Weber, 1932; *H. bischofi* Roemer, 1852; *H. crassimargo* Novák, 1890; *H. hastatus* Lütke, 1965; *H. montagnei* Hawle and Corda, 1847; *H. sculptus* Hawle and Corda, 1847; *L. vektori* Doubrava, 1991; *H. venetus* Gortani, 1915; *H. sp.* (Ancygin 1977); *H. sp.* (Alberti 1981); *H. sp.* (Alberti 1969); *L. sp.* (Rabano and Gutierrez-Marco 1993).

Cladistic analysis

Outgroups

Hibbertia and *Eoharpes* are used as outgroups in

the *Lioharpes* analysis. *Eoharpes* displays plesiomorphic characters of *Lioharpes*, such as small eyes and alae. *Hibbertia* shares the ornate brim and palpebral lobes, wide brim, anterior boss, vaulted glabella and large alae. *Hibbertia*, however, lacks the shallow to sunken alae and inflated genal roll common in most species of *Lioharpes*. The type species, *Hibbertia flanaganii* and *Eoharpes primus*, are selected as outgroups. *Lioharpes altaicus*, *L. bischofi*, *L. venetus* and *L. sp.* 1–4 are based on incomplete fragmentary material and have been excluded from the analysis to avoid unnecessary ambiguity.

Character states are listed in Table 6.

Characters

There are only three species (*L. crassimargo*, *L. hastatus*, and *L. venulosus*) of the 13 known species of *Lioharpes* that have fully preserved cephal. Ornament, prolongation length, glabellar shape, position of eyes, direction of eye ridges are similar in these three species. The characters below are the few which distinguish individual species of *Lioharpes*.

0. *Presence of sagittal ridge.* A ridge is continuous from the base of the glabella, opposite L1 to the frontal lobe. Sagittal crest present in *Hibbertia* and absent in *Eoharpes*.

0 absent; 1 present.

1. *Presence of sunken alae.* Sunken alae is defined as being lower than the genal area, as deeply set as the alar furrows. State 0 are either vaulted alae as in *Hibbertia* or, flat alae that are distinguished by the outline of the alar furrow as in *Eoharpes*.

0 absent; 1 present.

2. *Presence of continuous alar furrow.* Defined as an alar furrow continuous with the posterior border furrow. The alar furrow may join the posterior border furrow immediately below the ala.

0 absent; 1 present.

Results and Discussion

Standard parsimony analysis yielded an unresolved consensus of six trees (length=9, ci 100,

Table 6 Data matrix for *Lioharpes*.

	0 1 2
<i>Eoharpes</i>	0 0 0
<i>Hibbertia</i>	1 0 1
<i>L. hastatus</i>	0 0 1
<i>L. montagnei</i>	0 1 1
<i>L. sculptus</i>	1 0 0
<i>L. vektori</i>	0 1 1
<i>L. venulosus</i>	1 1 0

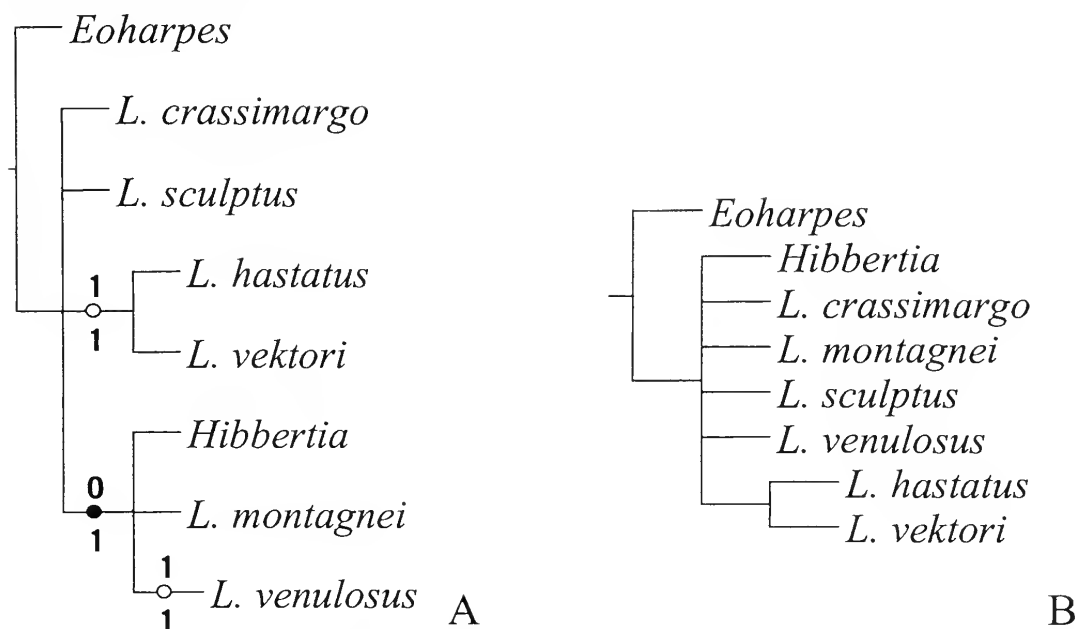


Figure 11 Standard parsimony analysis of *Lioharpes* found six equally parsimonious trees (length = 9, ci 100, ri 100). A. First tree; B. consensus.

ri 100) (Figure 11). Three-item analysis found one minimal tree (length=9, ci 100, ri 100) (Figure 12) in which the Middle Devonian *L. hastatus* from the Harz region of Germany, nested with the Lochkovian *L. venulosus* and the Silurian *L. vektori* from Bohemia.

Eight taxa from three areas provide some information on biogeography, namely, Middle Devonian Germany is more closely related to Lochkovian Bohemia than it is to Silurian Bohemia.

The small analysis is included to show the lack of data prevalent in such well known groups as *Lioharpes*. Despite the lack of morphological characteristics, a cladistic analysis, no matter how small, is still possible.

The standard parsimony analysis provides evidence for a non-monophyletic *Lioharpes* as *Hibbertia* is included in the ingroup in each analysis. *Lioharpes*, however, remains monophyletic in the three-item analysis. The conflict in the results of both analyses is due to the implementation of the methods and the small number of characters (evidence) used. A future analysis run with a greater number of characters and specimens is needed before the paraphyly of *Lioharpes* can be substantiated.

Genus *Scotoharpes* Lamont, 1948a
Figure 2G

Aristoharpes Whittington, 1950a: 11.

Selenoharpes Whittington, 1950a: 10.

Type species

Scotoharpes domina Lamont, 1948a; Llandovery (Lower Silurian), Scotland.

Diagnosis

Cephalon suboval to subcircular; prolongations almost straight or curving adaxially. Glabella longer than wide, with strong preglabellar and axial furrows. Anterior two pairs of glabellar furrows short and very shallow; posterior pair relatively deep. Preglabellar field short (sag.), flat. Eyes opposite anterior of glabella. Alae low, semicircular. Genal roll with low anterior boss. Brim gently concave or flat; girder prominent, meeting lower internal rim some distance in front of prolongation. Genae and fringe with pits separated by branching caeca. Single rows of larger pits developed against girder and upper and lower rims. Hypostome sagittally elongate. Thorax with at least 17 segments.

Remarks

The original diagnosis of *Scotoharpes* by Lamont (1948a: 376–377), which was based on a poor specimen from the Pentland Hills, Scotland, is inadequate. The descriptions of *Selenoharpes* and *Aristoharpes* that were later synonymized with *Scotoharpes* (Norford 1973), serve as better diagnoses for *Scotoharpes*-type specimens.

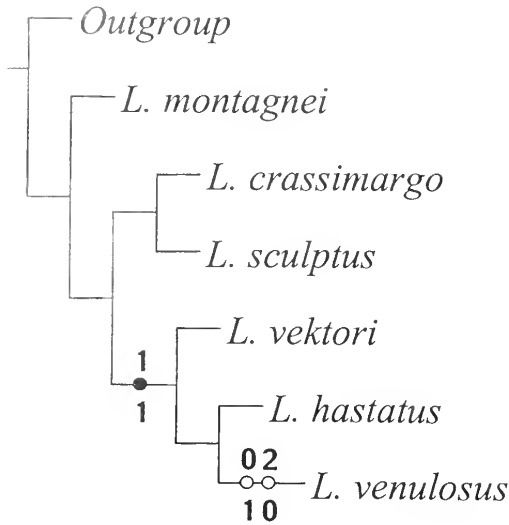


Figure 12 Single minimal tree (length = 9, ci 100, ri 100) yielded from a three-item analysis of *Lioharpes*.

Species Included

Scotoharpes aduncus Fortey, 1980; *Harpes cassinensis* Whitfield, 1897; *H. consuetus* Billings, 1863; *H. excavatus* Linnarsson, 1875; *S. filiarum* Dean, 1979; *Eoharpes fragilis* Raymond, 1925; *Harpes granti* Billings, 1865; *H. judex* Marr and Nicholson, 1888; *H. latior* Poulsen, 1934; *S. laurei* Jell and Stait, 1985; *H. tobulatus* Chugaeva, 1975; *S. loma* Lane, 1972; *S. molongloensis* Chatterton and Campbell, 1980; *H. pansa* Maksimova, 1960; *S. planilimbatus* Lu, 1975; *S. raaschii* Norford, 1973; *Aristoharpes rotundus* Bohlin, 1955; *Hibbertia sanctacrucensis* Kielan, 1960; *Harpes sinensis* Grabau, 1925; *Selenoharpes singularis* Whittington, 1965; *Scotoharpes sombrero* Owen, 1981; *H. spasskii* Eichwald, 1840; *Aristoharpes taimyricus* Balashova, 1959; *Selenoharpes tatouyangensis* Chang and Fang, 1960; *Harpes telleri* Weller, 1907; *H. trinucleoides* Etheridge and Mitchell, 1917; *Scotoharpes vetustus* Zhou and Zhang, 1978; *Selenoharpes vitilis* Whittington, 1963; *Scotoharpes volsellatus* Howells, 1982; *Aristoharpes willsi* Whittington, 1950a; *Harpes (Eoharpes) youngi* Reed, 1914; *S. sp.* (Norford 1973); *A. (?) sp.* (Whittington 1950a); *S. (?) sp.* (Bordet et al. 1960); *H. (?) sp.* (Dean 1970); *H. (?) sp.* (Bates 1968); *H. (?) sp.* (Kobayashi and Hamada 1972); *H. (?) sp.* (Owen and Bruton 1980); *H. (?) sp.* (Thomas 1978); *H. (?) sp.* (Ingham 1970); *H. (?) sp.* (Ross 1972); *H. (?) sp.* (Lane 1979).

Cladistic analysis

The cladistic analyses below are restricted to 21 of the 43 known and described species. The majority of species were based on fragmentary material,

insufficient for use in a cladistic analysis. Character states are tabulated in Table 7.

Outgroups

The type species *Eoharpes primus* and *Bohemoharpes naumanni* were chosen as outgroups for the *Scotoharpes* analysis. All genera share the vaulted glabella, small alae, coarsely pitted rim and prolongations. *Scotoharpes* consists of a varying degree of morphology that can be attributed to either *Eoharpes* or *Bohemoharpes*. The outgroups represent two possible ancestors to *Scotoharpes*. These characteristics will assist in assessing the monophyly of *Scotoharpes*.

Characters

0. *Cephalon shape*. Cephalon shape varies considerably in *Scotoharpes*. Three basic shapes can be determined; squat, rectangular or anteriorly expanded variants. Semicircular cephalons do not have strongly adaxially curved prolongations, and ovate brims may have a rectangular shape. *Eoharpes* and several *Bohemoharpes* species have a typically semicircular shape. Ovate, circular cephalons are possibly derived from a semicircular shape.

0: Semicircular shaped; 1: ovate; 2: circular

1. *Brim length*. Measured as the length of the brim anteriorly (sag.) against the length opposite eye (lat.). Brim length is even in *Eoharpes* and varied in

Table 7 Data matrix for *Scotoharpes*. '?' indicates missing data.

	012345678911111111112222222
	01234567890123456
<i>Eoharpes</i>	010000010100000000012000100
<i>Bohemoharpes</i>	2000100??0000?00000?0011?0
<i>S. cassinensis</i>	101101112000000010001101100
<i>S. consuetus</i>	1000010?20000001?00?0?21111
<i>S. domina</i>	000011122010011000112110110
<i>S. excavatus</i>	??1?1?1?0000011??0?0?0???
<i>S. filiarum</i>	0?000?1?20122101?1111000111
<i>S. fragilis</i>	?100011?20000?0000000000000
<i>S. judex</i>	1100??02?0?0??100111111?0
<i>S. latior</i>	??1000021001110?00000000000
<i>S. laurei</i>	210001002100000100001001111
<i>S. loma</i>	010?1012000011010102100100
<i>S. molongloensis</i>	100110022000001010112100110
<i>S. planilimbatus</i>	21000??2?00000000000000011
<i>S. raaschii</i>	0??1010?200110001111210?1??
<i>S. cf. raaschii</i>	0111010020010010111121011??
<i>S. singularis</i>	10001000200000?0?0??0?21110
<i>S. sombrero</i>	1001111221000101001110211?0
<i>S. telleri</i>	1001110?00??100?11?001110
<i>S. trinucleoides</i>	1000110220000??00112111111
<i>S. vitilis</i>	1110011020100011?1100001110
<i>S. willsi</i>	10011??2200000?0001121211??
<i>S. youngi</i>	1001100020000?00?0??0?1111?0

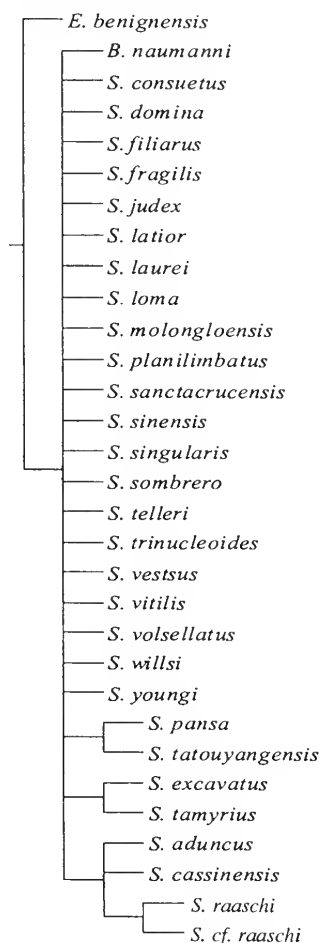


Figure 13 Standard parsimony analysis of *Scotoharpes*. A strict consensus of 878 most parsimonious trees (length = 120, ci 27, ri 56).

Bohemoharpes.

0: even; 1: uneven

2. *Fringe concavity (sag.)*. See description in *Bohemoharpes* character analysis above.

0: absent; 1: present

3. *Brim slope*. Measured sagittally in lateral view. Species that show any sign of anterior slope code as state 1. Brims with sagittal concavity may show both posterior and anterior slope. Unless there is a distinct anterior slope, concavity is not considered to show presence of slope. *Eoharpes* has a flat brim with no slope, whereas slope varies greatly in *Bohemoharpes*.

0: no slope; 1: gentle slope

4. *Presence of axial furrow extension*. No known species of *Scotoharpes* has an anterior boss. However, several species show the anteriorly

extended axial furrows onto the genal roll, a possible plesiomorphic state of an anterior boss. *Eoharpes* lacks axial extensions and/or boss, present in both *Bohemoharpes* and *Scotoharpes*.

0: absent; 1: present

5. *Presence of anterior glabellar depression*. The preglabellar furrow is continuous with an anterior glabellar depression. The depression extends sagittally along the genal roll and girder. The depression can be distinguished from the preglabellar field by the transverse preglabellar field.

0: absent; 1: present.

6. *Transverse preglabellar ridge*. A difference in depth/concavity of the preglabellar field and genal depression leads to a ridge system that runs parallel to the preglabellar furrow. The transverse preglabellar ridge forms when the genal depression is deeper and/or longer (sag.) than the preglabellar furrow. This character is unique to several species of *Scotoharpes*.

0: absent; 1: present

7. *Course of inner margin or fringe (sag.)*. See Character 3 in *Bohemoharpes* character analysis.

0: straight; 1: concave; "W" shaped

8. *Course of eye ridge*. Unlike *Bohemoharpes*, eye ridges are distinct in *Scotoharpes* and occur as three variants. Adaxial ridges only occur between the axial furrow and eye; adaxial ridges either efface along the palpebral margin, or are continuous with the inner margin. *Eoharpes* and most *Bohemoharpes* species have an adaxial eye ridge.

0: adaxial; 1: effacing abaxially; 2: continuous with inner margin

9. *Glabellar shape*. The majority of glabellae in *Scotoharpes* are bullet-shaped with a variety of sizes, ranging from squat, vaulted to elongate and narrow. Herein angular, strongly tapering glabella are coded as [9: 1].

0: bullet shaped; 1: triangular

10. *Sagittal crest*. This is a distinct ridge that runs along the glabella, that in rare cases may extend on to the genal roll. Extension of the crest may eliminate the possibility of a preglabellar furrow or genal depression. Sagittal crests occur only on elongate, bullet shaped glabella and may act as a strengthening structure. Both outgroups lack a sagittal crest.

0: absent; 1: present

11. *Condition of S3*. S3 and S2 occur in at three separate levels of development. An undeveloped or absent furrow is common in *Scotoharpes* and both outgroups; adaxially effacing furrows become

shallower adaxially; medially extended furrows have a constant depth and in the case of S3 are continuous, with S2 abaxially and anterolaterally directed.

0: not developed/absent; 1: effacing adaxially; 2: effacing medially

12. *Condition of S2*. S2 is laterally directed in state 2.

0: not developed/absent; 1: effacing adaxially; 2: effacing medially

13. *Shape of S1*. See Character 6 in *Bohemoharpes* analysis. The posterolaterally directed S1 may have two shapes: that of a straight line and a curve in the shape of a 'J'0: straight; 1: 'J'-shaped

14. *S0 depth (sag.)*. S0 depth sagittally or no continuity in S0 depth, occurs with the increase in L0 development. Anteriorly or posteriorly directed L0 may change in length (sag.) or become vaulted. This condition is similar to the extension of the glabellar crest and the decrease in depth of the preglabellar furrow in *Kielania neogracilis* (Richter and Richter 1924). L0 development in *Eoharpes* and *Bohemoharpes* is minimal and S0 depth generally continuous.

0: shallow sagittally; 1: even depth

15. *Condition of L0 (sag.)*. Sagittally, L0 can be either anteriorly or posteriorly directed. Direction is measured as the direction of the most convex sagittal margin of L0. Convexity of L0 is minimal in both outgroups.

0: posteriorly directed; 1: anteriorly directed

16. *Alar depression*. Alar depressions are formed by the anterior widening (tr.) of the alar furrow opposite the axial furrow. The alar depression is usually longer (exsag.) than it is wide (tr.) and does not exceed the depth of the alar furrow. Species without alar depressions have furrows with continuous length. Alar depressions are common in *Scotoharpes*, but do not occur in genera with smaller unpronounced alae. Alar depressions are absent in both outgroups.

0: absent; 1: present

17. *Posterior alar depression*. The posterolateral lengthening (exsag.) of the alar furrow is known as the posterior alar depression. The posterior alar depression is not as common as the alar depression in Character 16 and may be confused with an alar furrow continuous with the posterior border furrow at its most posterior point (exsag.). The posterior alar depression forms laterally to the ala and extends posterolaterally into the posterior border furrow. The area is usually large, equal in depth to the alar furrow and free of any ornament. Posterior alar depressions are absent in both outgroups.

0: absent; 1: present

18. *Alar inflation*. Alar inflation refers to any relief of the alae. Alae may remain flat, equal in relief to the furrow, either appearing as a faint outline in a large depression or flat surface lateral to the L1. Alar inflation should not be confined to a vaulted ala rising steeply toward L1.

0: absent; 1: present

19. *Alar direction*. Measured as the direction of the posterior alar furrow versus the lateral axis perpendicular to the sagittal. Alae are either parallel or are anterolaterally directed at different angles below 45 degrees. Most alae are asymmetrical and direction is clearly noticeable, however with symmetrical alae, direction is measured as the bilateral axis. Most symmetrical alae are laterally directed.

0: laterally directed; 1: anterolaterally directed

20. *Alar size*. Alar size is measured in relation to L1, not cranium size. Hence species with [20: 2] may not actually possess large alae in comparison with other larger species. Measuring ala versus L1 size is justified as both characters are independent, although both are treated as dependent for the purposes of coding.

0: small; 1: equal; 2: large

21. *Length of posterior border (exsag.)*. Measured posteriorly to alae (exsag.) and in relation to S0. For the purpose of coding in cases where S0 is not preserved, a long posterior border is not usually associated with long (exsag.) posterior border furrows.

0: narrow; 1: long

22. *Prolongation length (exsag.) versus cephalic length (sag.)*. Prolongation length is measured sagittally as the distance from L0 to the level of the prolongation spine/tip, against the anterior border (sag.) to L0 (sag.).

0: less; 1: equal; 2: more

23. *Internal rim concavity of prolongation*. Measured as the concavity of the internal rim of the prolongation excluding the tip/spine.

0: straight; 1: convex

24. *External rim convexity of prolongation*. Measured as the convexity of the external rim of the prolongation, excluding the tip/spine.

0: straight; 1: convex.

25. *External rim length on prolongation*. A thick rim lacks a wide rim furrow and is usually thicker than it is high. Narrow rims usually have a wide concave border. Prolongations possessing spines either have both a thick internal and/or external rim.

0: narrow; 1: wide

26. *Presence of prolongation spines*. Measured as the posterior extent of the external and/or internal rim.

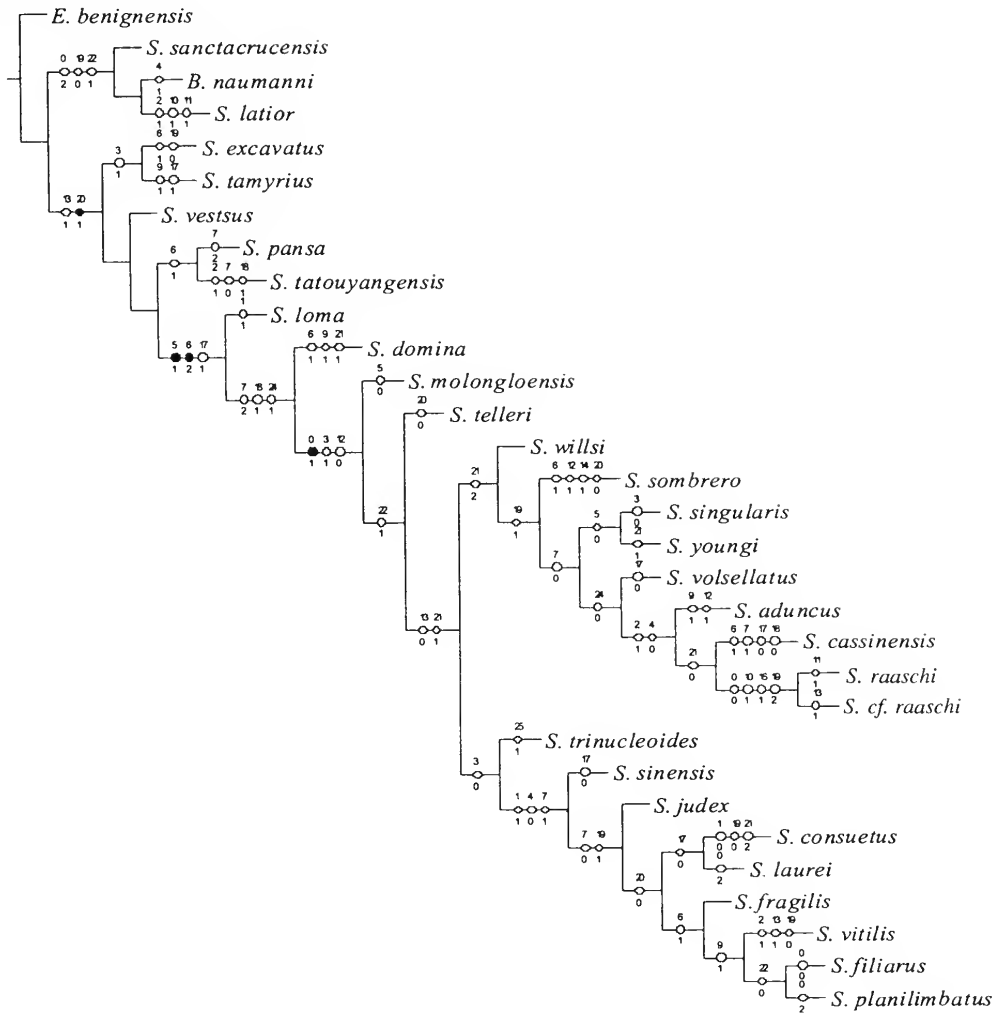


Figure 14 Characters mapped onto first tree of the *Scotoharpes* standard parsimony analysis (length = 120, ci 27, ri 56).

The presence or at least one thickened rim margin is necessary for spine formation. Both outgroup taxa lack spines.
0: absent; 1: present

Results and Discussion

Standard parsimony yielded a consensus of 878 most parsimonious trees (length = 120, ci 27, ri 56) consisting of four resolved nodes (Figure 13). Characters are mapped on to the first tree in Figure 14. Three-item analysis yielded a minimal cladogram (length = 7995, ci 67, ri 52) (Figure 15).
The minimal tree consists of a predominantly Silurian clade containing nine species, of which two are biogeographically and stratigraphically ambiguous, as *S. molongloensis* is found in the

Middle Silurian of Australia and *S. cassinensis* in the Lower Ordovician of Vermont, USA. The remaining seven species span from the Ordovician of the United Kingdom to the Silurian of Alaska. This clade is basal to the Sino-Australian-Laurentian clade that includes the type species *S. domina*.
Standard parsimony consensus places *Bohemoharpes* in the ingroup, whereas the three-item analysis keeps a monophyletic ingroup. These differing results are due to the differences in implementation. *Scotoharpes* may very well be non-monophyletic and consist of several monophyletic groups. *Scotoharpes*, like *Harpes*, has also been used as a taxonomic dumping ground for taxa or partially preserved taxa. The characteristics

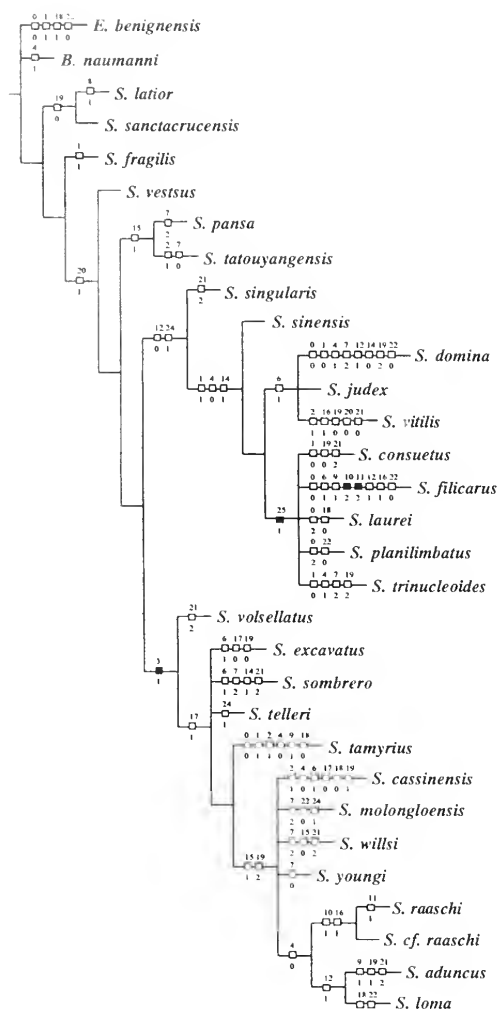


Figure 15 Three-item analysis of *Scotoharpes* yielded a minimal tree of 216 most parsimonious trees (length = 7995, ci 67, ri 52).

attributed to *Scotoharpes* are so variable that there are no unique *Scotoharpes* characteristics. This is seen in the similarities that some taxa share with *Bohemoharpes* and others with *Eoharpes*. A new cladistic analysis of *Scotoharpes* is needed. The new analysis should include a larger number of new specimens that are better preserved. Until such an analysis is attempted there can be no certainty over the monophyly of *Scotoharpes*.

Ordovician species are found both at basal and topographically higher nodes. A stratigraphically mixed clade should not be void if it does not conform to our knowledge of the stratigraphic record. By using stratigraphy to confine our taxa we bias our result. The presence of deeply nested

Ordovician sister taxa in a Silurian clade, or sister taxa of varying ages only highlights the amount of missing data.

NOMEN DUBIA

Arraphus corniculatus Angelin, 1854; *Australoharpes precordilleranus* Baldi and Gonzalez, 1986; *Harpes antiquatus* Billings, 1859; *Harpes bucco* Bather, 1910; *Harpes concavus* Thorslund, 1940; *Harpes costatus* var. *actua* Weber, 1948; *Harpes gotlandium* Kegel, 1927; *Harpes kyliandrorhachis* Kobayashi and Hamada, 1972; *Harpes minnestoensis* Clarke, 1897; *Harpes pamiricus* Balashova, 1966; *Harpes pygmaeus* Lütke, 1965; *Harpes scanicus* Angelin, 1854; *Harpes speciosus* Münster, 1840; *Trinucleus ellipticus* Münster, 1840; *Trinucleus issedon* Eichwald, 1857; *Trinucleus laevis* Münster, 1840; *Harpes pruniformis* Alberti, 1969.

NOMINA NUDUM

Harpes latilimabtus coll. Krause (1885).

ACKNOWLEDGEMENTS

We are grateful to David M. Williams and Gregory D. Edgecombe for critically reviewing this manuscript. We are also grateful to Richard Fortey, Raimund Feist, Petr Budil, Jana Slavickova, Thomas Becker, Karsten Weddige, Rod Long and Frau Dörner for their help and assistance. M.C.E. also wishes to thank the Western Australian Museum for support and the University of Melbourne for funding and the Alfred Nicholas Travel Scholarship. We wish to thank Alan Owen for the provision of the photograph of the type specimen of *Dubhglasina aldonsensis*. Alex Stevens and Alex Baynes are thanked for their editorial assistance.

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Seasonality of beachwrack at Oakajee in the mid-west region of Western Australia

Fred E. Wells

Western Australian Museum Perth, Western Australia 6000, Australia
Email: wells@museum.wa.gov.au

Abstract – This study examines seasonal fluctuations in beachwrack accumulations near Oakajee, Western Australia (28°34'S; 114°34'E). Twelve monthly samples were made of beachwrack concentrations at Drummonds Cove and Coronation Beach from 5 May 1998 until 10 April 1999. Four weekly samples were made from 23 July to 12 August 1998 to measure short-term variations in beachwrack volumes. There was no seasonality in beachwrack accumulations at Drummonds Cove. At Coronation Beach beachwrack concentrations were high in late summer and early winter, but declined sharply from late winter to early spring. There was considerable movement of wrack onto and off the beaches. Beachwrack accumulations migrated along the beach within Drummonds Cove, but there was no evidence of such longshore movement on the open coast. Beachwrack accumulates in bays and other protected areas and at the tip of peninsulas, such as Point Moore. Macroalgae and the seagrass genera *Amphibolis* and *Posidonia* dominated the wrack.

Keywords: beachwrack, macrophytes, Western Australia, seagrass, seaweeds, macroalgae

INTRODUCTION

Oceanic waters off Western Australia are nutrient poor, at levels characteristic of the open ocean. Consequently, phytoplankton production is minimal (Rochford, 1980; Pearce 1991; 1997). Instead benthic plants, both seagrass and macroalgae, provide most of the primary production. The plants are torn from the bottom during storms and then moved about by currents and waves. A portion is transported to shore where it accumulates as beachwrack. The beachwrack is reworked by wind and waves, accumulating in some areas and being absent in others. It is mobile, often alternating between the water and the beach. Volumes change considerably over short periods of time (Hansen, 1984).

Beachwrack in the Perth area develops an abundant invertebrate fauna which feeds on it. The invertebrates are dominated by amphipods, particularly *Allorchestes compressa* (Robertson & Lucas, 1983; McLachlan, 1985; Fong, 1999). Nearshore the beachwrack and associated invertebrates provide shelter and food for a variety of fish species (Lenanton, 1982; Lenanton et al., 1982; Robertson & Lenanton, 1984), including the commercially important cobbler *Cnidogobius macrocephalus* (Lenanton & Caputi, 1989), and abalone (Wells & Keesing, 1989). Nutrients are released back into the water column as the

beachwrack decomposes (Robertson & Hansen, 1982). This recycling is important in the low nutrient environment off Western Australia.

The present study extends our knowledge of beachwrack accumulations to Oakajee, just north of Geraldton. The study tested the hypotheses that beachwrack accumulates seasonally, with a maximum due to winter storms, and once on the beach, the beachwrack migrates longshore in response to prevailing wave and wind directions.

THE OAKAJEE MARINE ENVIRONMENT

The Oakajee region (Figure 1) is an open, exposed coastline subject to the full force of sea conditions, particularly during storms. It is thus a very high energy environment. Virtually the entire shoreline from Geraldton north to the mouth of the Bowes River is composed of intertidal sand. Beachrock platforms occur along the shoreline throughout the Oakajee region but are more common north of the Oakabella River. They range from small platforms of a few square metres to an extensive platform just south of Coronation Beach. The platforms begin at the low tide level and continue into the subtidal region. Large portions may be exposed by winter wave action then recovered by sand the following summer. The platforms at Oakajee have a greatly reduced biota, possibly due to the dynamic wave

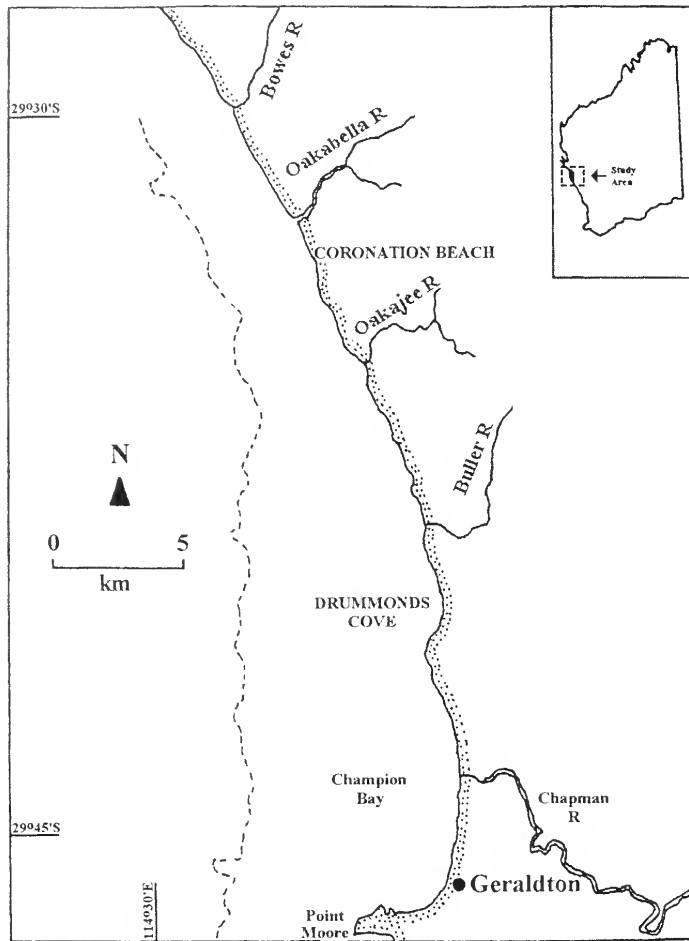


Figure 1 Map of the Oakajee coastline showing localities mentioned in the text.

action at Oakajee that would physically remove much of the macroalgae and fauna. In addition, sand moved about by the waves would provide a considerable scouring force.

In the nearshore environment the substrate is limestone that may or may not be covered with sand. While considerable local variation in depth occurs, there is a steady progression of habitats from the intertidal sand beach out to the 20 m line. A shallow lagoon up to 5 m deep occurs near the shore. The lagoon is more distinct south of the Oakajee River. North of the Oakajee, the lagoon is less distinct and has numerous bombies, many of which nearly reach the sea surface. An indistinct limestone reef occurs to the west of the lagoon. The reef runs north to south parallel to the shore, and is absent only off the mouth of the Oakajee River. In most areas the reef shoals to a depth of 2 m or less, but in some localities it is less distinct.

Seaward of the reef crest is a low relief platform. While the platform surface is not uniform, it tends to have a gradually increasing depth seaward. Small crevices and depressions occur throughout the surface of the limestone. The platform is channelled with a very small spur and groove formation in some areas, where the undulations may be 30 cm or less in height. The surfaces of the crest are exposed limestone. The channels are either exposed limestone or are covered by a thin layer of sand. Sand accumulates in the depressions, some of which are large, tens of metres across. In some low energy areas of the bottom the entire limestone platform is covered by a layer of sand several centimetres deep. In deeper waters, where depths are between 15 and 20 m, the platform gives way to a level bottom that is predominantly covered with sand, but there are exposed areas of flat limestone.

The bottom habitats can change considerably over

a space of a few metres, particularly in the shallow inshore waters and the high relief reef. Over a space of 100 to 200 m going seaward, the bottom can vary from high relief reef with sand patches in the depressions, to a low relief reef dominated by the seagrass *Amphibolis antarctica*, to areas co-dominated by *A. antarctica* and macroalgae, to areas where only macroalgae are present. There may also be sandy bottoms where *A. antarctica* forms a dense seagrass meadow. The ability of *A. antarctica* to live on either sandy or rocky bottoms is well demonstrated at Oakajee.

Shallow vertical columns, which occur near the shore south of the Oakajee River, are one of the most distinctive features of the marine environment in the Oakajee area. The columns, which may have a diameter of 5–10 m or more, emerge vertically from sand at a depth of up to 5 m to near the lower intertidal level. This is an area of breaking waves during even moderate seas. The upper surfaces of the columns are largely devoid of macroalgae, but may be colonised by small patches of *Sargassum* which are kept to short lengths by the continuous wave action. The *Sargassum* is longer on the sides of the columns than on the upper surfaces. On the leeward side of the columns is a mixture of low encrusting species of macroalgae, including *Caulerpa*. The base of the columns is at a depth of approximately 6 m and is surrounded by sand mixed with some *Amphibolis*. There may be small patches of *Sargassum* inshore. Invertebrate diversity on the tops of the columns is low.

MATERIALS AND METHODS

Twelve aerial flights were made at approximately monthly intervals over the coastline at Oakajee (28°34'S; 114°34'E) from 5 May 1998 until 10 April 1999 using a Cessna 172 aircraft. Most flights were made at 140–165 km h⁻¹ at an altitude of 100 m from south of the Port of Geraldton to the mouth of the Bowes River, a distance of approximately 40 km. A video recording was made of the entire shoreline on the flight north. A still camera was used on the flight south to photograph major beachwrack accumulations. Four weekly flights were made from 23 July to 12 August 1998 to measure short-term variations in beachwrack volumes.

The only major accumulations of beachwrack on the first flight were at Drummonds Cove and at Coronation Beach. As vehicle access to the shore was possible, the two beaches were chosen for ground truthing. On most occasions the two sites were the locations with the greatest beachwrack concentrations. Methods used by Hansen (1984) were used to determine beachwrack volumes on the shoreline. Length and width of beachwrack accumulations at Drummonds Cove and at Coronation Beach were measured. Length was

stepped off and compared with the number of steps required to cover a known distance. Width and depth were measured at consistent intervals with a tape measure marked to the nearest 1 cm. The intervals were calculated to provide at least 6 measurements at each of the two localities; usually 8–10 measurements were made. Width of beachwrack was measured to the nearest 10 cm from the seaward to the landward edge of the beachwrack. Depth was normally measured to the nearest 1 cm at three locations: top of the seaward beachwrack crest, middle of the accumulation, and the landward margin; only two measurements of depth were made in small accumulations where there was little beachwrack present. Total volume of beachwrack on each beach was then calculated.

To measure the composition of beachwrack, four samples were collected each at Drummonds Cove and at Coronation Beach on 12 June 1998 and 16 January 1999, placed in labelled plastic bags and frozen until analysis. Samples were collected from freshly deposited areas of wrack to minimise the proportion of unidentifiable detritus. The samples were washed in freshwater then sorted to five major plant types: macroalgae, the seagrass genera *Amphibolis*, *Posidonia* and *Halophila*, and unidentified plant material. Individual components were placed on aluminium foil and dried for 48 hours in a drying oven at 80°C. They were then weighed to the nearest 1 mg on a Sartorius electronic balance.

RESULTS

The greatest accumulations found during the first survey on 5 May 1998 were at Drummonds Cove, where 7559 m³ of beachwrack occurred on the shoreline, and at Coronation Beach, where there was 2477 m³ (Figure 2). Smaller accumulations occurred in other areas. Accumulations at Drummonds Cove were consistently the largest along the shoreline between Drummonds Cove and the Bowes River, some 25 km of coastline.

Seasonal variation

The predicted pattern of seasonality was not clearly demonstrated at Drummonds Cove during the study (Figure 2). The accumulation at Drummonds Cove on 7 May 1998 was spread over an estimated 1786 m of beach. As expected, the beachwrack increased to 8510 m³ on 12 June, but instead of continuing to increase during the winter, wrack volumes declined sharply, reaching a low of 817 m³ on 6 August. Wrack accumulations at Drummonds Cove increased to 3154 m³ one week later on 13 August. They continued to increase until 9 October, when a peak of 7436 m³ was reached. Significant accumulations remained for the remainder of the study, varying from 3196 m³ to 5780 m³ over

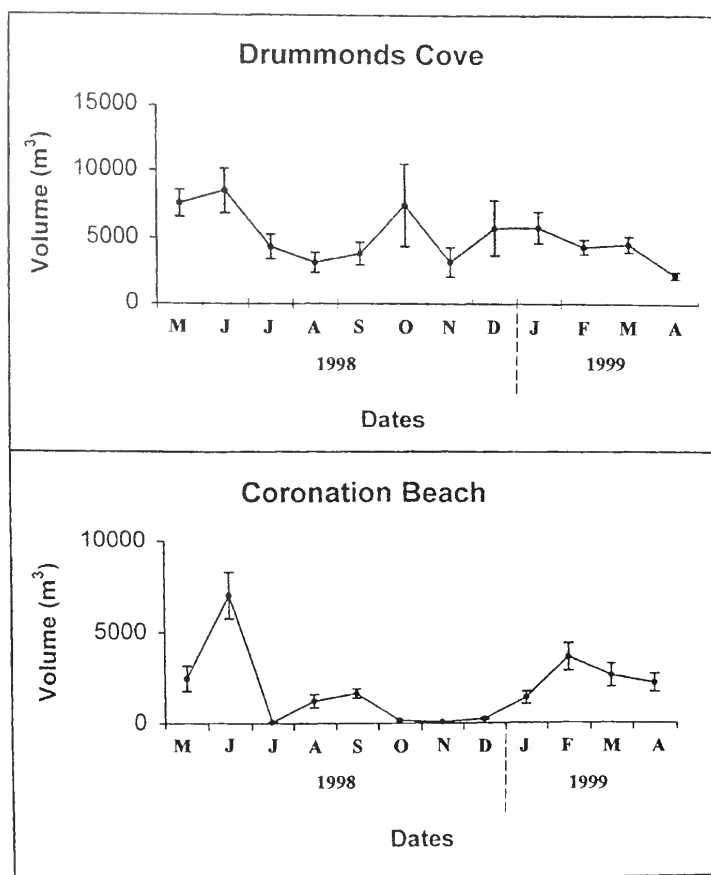


Figure 2 Seasonal patterns of accumulation of beachwrack at Drummonds Cove and Coronation Beach from May 1998 to April 1999. Means and standard errors are shown.

summer, declining to 2221 m³ on the final month of the survey (10 April 1999).

In contrast, the pattern at Coronation Beach was seasonal (Figure 2). Accumulations totalled 2477 m³ on 7 May 1998 and were along 629 m of beach. The beachwrack increased significantly to 7043 m³ on 12 June. During the period of late winter to early summer beachwrack at Coronation Beach declined to low levels, ranging from 58 m³ on 23 July to 443 m³ on 11 September. Beachwrack volumes increased sharply to 3647 m³ on 20 February (late summer) and remained relatively high for the duration of the study.

Short-term variation

Considerable short-term variation was found during the four week intensive survey at Drummonds Cove (Figure 3). Concentrations at Drummonds totalled 4372 m³ on 23 July. Two weeks later they had dropped to 817 m³. Beachwrack increased during the next week to 3154 m³.

In contrast to Drummonds, the four week intensive survey at Coronation Beach showed little variation in beachwrack concentrations (Figure 3). During the first three weeks (23 July, 30 July and 6 August) there was essentially no beachwrack present. An increase to 1221 m³ occurred by 13 August.

Longshore movement

There was no clear evidence of longshore movement of beachwrack along the Oakajee coastline, but the rapidly changing volumes, particularly during the short term study at Drummonds Cove, showed that there is considerably flux in wrack between the shore and the offshore waters.

At the beginning of the study, beachwrack occupied much of the bay at Drummonds Cove. It moved several hundred metres to the north during the winter and early spring, but remained in Drummonds Cove. In spring fresh build-ups

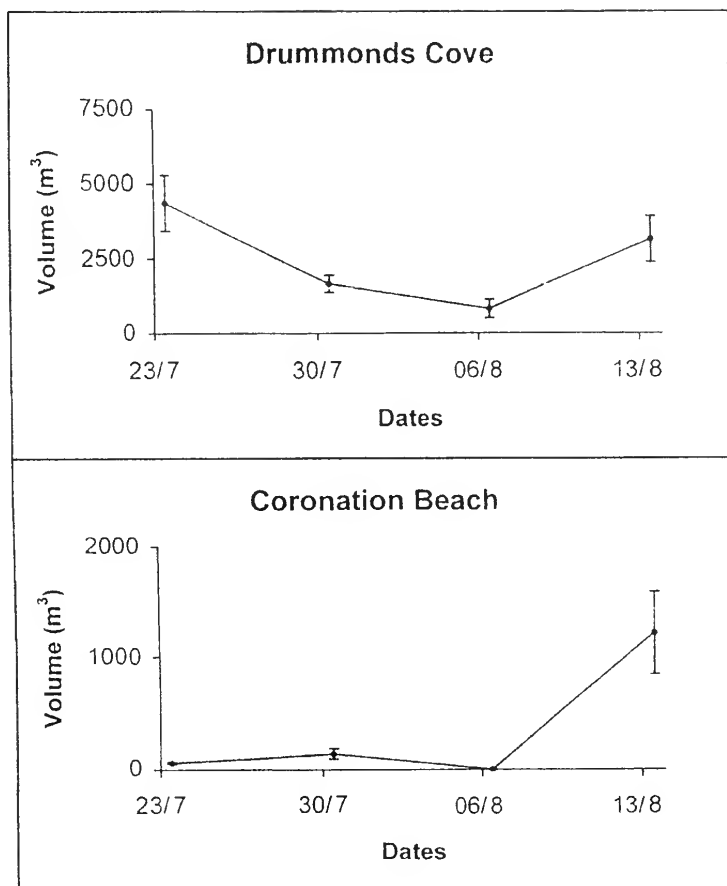


Figure 3 Short-term variations in accumulation of beachwrack at Drummonds Cove and Coronation Beach in July and August 1998. Means and standard errors are shown.

Table 1 Composition of beachwrack at two locations along the Oakajee coastline in winter 1998 and summer 1999.

	Algae	Seagrasses			Detritus	Total
		<i>Amphibolis</i>	<i>Posidonia</i>	<i>Halophila</i>		
DRUMMONDS COVE						
Winter 1998						
Mean (\pm SE) (gm)	10.5 \pm 1.5	3.9 \pm 0.3	2.7 \pm 0.8	0 \pm 0	3.8 \pm 1.3	20.9 \pm 3.1
Percentage	50.2	18.8	12.9	0.0	18.1	100.0
Summer 1999						
Mean (\pm SE) (gm)	11.5 \pm 1.7	8.8 \pm 1.4	0.7 \pm 0.2	0 \pm 0	2.3 \pm 0.7	23.3 \pm 0.9
Percentage	49.4	37.8	3.2	0.0	9.7	100.1
CORONATION BEACH						
Winter 1998						
Mean (\pm SE) (gm)	12.5 \pm 1.2	16.4 \pm 1.1	1.0 \pm 0.3	0 \pm 0	3.4 \pm 0.4	33.3 \pm 2.2
Percentage	37.6	49.1	3.0	0.0	10.2	99.9
Summer 1999						
Mean (\pm SE) (gm)	20.4 \pm 3.1	17.3 \pm 3.9	3.6 \pm 0.4	0 \pm 0	3.2 \pm 1.4	44.5 \pm 5.9
Percentage	45.9	38.8	8.1	0.0	7.2	100.0

developed along the southern shoreline of Drummonds Cove and remained there for the duration of the study.

At Coronation Beach two accumulations during May 1998 were on the northern and southern ends of the beach. The southern accumulation disappeared by June. The beachwrack to the north increased in June, but then decreased over time. Beachwrack accumulations increased over summer, and by February the entire margin of the bay was fringed with beachwrack.

There was no longshore movement of other beachwrack accumulations or drift macroalgae viewed during the aerial surveys. In particular, a major accumulation of beachwrack south of the mouth of the Chapman River remained at consistently high levels and maintained a constant position. The aerial surveys found beachwrack accumulations on the southern shoreline of the port of Geraldton, but they were not substantial. The aerial examination and several shoreline searches demonstrated that beachwrack also accumulates along the Geraldton beaches just north of the port. The mouth of the Chapman River consistently had the largest accumulations south of Drummonds Cove. These were measured on 5 December 1998, and had an estimated volume of 4907 m³, somewhat smaller than the accumulation of 5780 m³ at Drummonds Cove on the same day. The western tip of the port of Geraldton has a small bay near the southern tip of the peninsula; this area regularly trapped beachwrack.

DISCUSSION

The pattern of beachwrack accumulations varied between Drummonds Cove and Coronation Beach. There was no seasonality at Drummonds Cove. In contrast, at Coronation Beach beachwrack concentrations were high in late summer and early winter, but declined sharply from late winter to early spring. Experience in other areas of Western Australia has been similarly mixed. Some areas have winter maxima, but others do not. Beachwrack accumulates seasonally during winter at the southern groyne at Port Geographe in Busselton (P. Collins, pers. comm). Kirkman (1984) reported considerable interannual variation in beachwrack quantities in the Marmion lagoon. Different patterns of seasonality occurred during the years studied. Hansen (1984) examined beachwrack along 46 km of coast from Triggs to Two Rocks, and found similar variability between sites, seasonally and between years. A series of photographs published by Kirkman & Kendrick (1997) also demonstrates high short-term variability in beachwrack concentrations. The results of all these studies demonstrate that the timing and magnitude of beachwrack accumulations are highly dependent on

local conditions and may vary considerably across a range of time scales (days/months/years) at a single location.

It was thought that once on the beach at Oakajee, the beachwrack would migrate north or south along the shore in response to prevailing wave and wind directions. This did occur within Drummonds Cove, but there was no evidence of such longshore movement on the open coast. Instead, the beachwrack accumulates in bays and other protected areas and at the tip of peninsulas, such as Point Moore. Working on the northern Perth beaches, Hansen (1984) obtained mixed results. Some sites had predictable, large quantities of beachwrack, which remained in the same area. Concentrations at other sites were less predictable and the beachwrack moved along the shoreline. Clear patterns of longshore movement occur in Geographe Bay. Beachwrack reaches the shore from Dunsborough to Busselton and moves northward along the shoreline until it reaches Port Geographe (P. Collins, pers. comm.). A major accumulation of 70–80,000 m³ occurred along the southern side of the development at the end of winter in 1998; it was prevented from moving northwards by the groyne.

Composition of beachwrack is variable, depending on the material available in the offshore environment. Beachwrack at Oakajee is a combination of macroalgae and the seagrass *Amphibolis*. Hansen (1984) found beachwrack in the northern portion of the Perth area to be composed of a variety of constituents, including the kelp *Ecklonia radiata*, seagrasses and numerous small macroalgae. In Hansen's (1984) study of the Perth area, *E. radiata* was dominant over a full year, followed by other macroalgae, then seagrass. *Sargassum* was seasonally important during summer.

Only a small proportion of detached macrophytes ends up on the beach. For example, Kirkman & Kendrick (1997) released 5000 tagged *Ecklonia radiata* in the Marmion Lagoon in winter 1985. The tagged plants took 15 to 23 days to reach shore, but only 53 (1%) were recovered on beaches. In her detailed study of beachwrack in the Perth metropolitan area, Hansen (1984) found considerable variation in the amount of beachwrack, from 1.3 to 45.3 kg dry weight per metre of coastline. On average there was 74 to 80 tonnes of carbon per kilometre of coastline, equivalent to about 18% of the nearshore macrophyte production. These figures emphasise that the material in the beachwrack is only a fraction of total macrophyte production in nearshore waters.

ACKNOWLEDGEMENTS

Caroline Bodenham of the Central West College

of Technical and Further Education provided considerable enthusiastic assistance in the field at Geraldton. In addition, Greg Burrows, Barbara Larkin, Priscilla Rodd, and David Wells each assisted on one trip. Contact with TAFE was through Steven Webster. Chris Shine and his pilots and staff at Shine Aviation Services provided skilful services during the low level overflights of the beaches at Oakajee. In addition the following people are thanked for their assistance in providing information on the project: Peter Collins and Ian LeProvost, LeProvost Dames & Moore; Dr Gary Kendrick, Department of Botany, University of Western Australia; and Kim Nardi and Randall Owens of Fisheries Western Australia, Geraldton. Dr Gary Kendrick and Dr Anne Brearley kindly commented on the manuscript, which substantially improved the paper.

This information was originally generated as part of a study of the potential effects of the construction of a new deepwater port at Oakajee. It was done under a contract between the Western Australian Department of Resources Development and LeProvost Dames & Moore (now part of URS Australia). I am grateful to DRD for permission to publish the information and to Peter Goodall and David Meehan at DRD for their considerable help and encouragement during the project.

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Biology of the Black-stripe minnow *Galaxiella nigrostriata*, (Galaxiidae) in an acidic, black-water lake in Melaleuca Park near Perth, Western Australia

Kimberly D. Smith^{1,2}, Brenton Knott¹ and Edyta J. Jasinska^{1,3}

¹ Department of Zoology, The University of Western Australia,
35 Stirling Highway, Crawley, WA 6009, Australia.

² Present address: Murdoch University Centre for Fish and Fisheries Research,
Division of Science and Engineering, School of Biological Sciences and Biotechnology,
Murdoch University, Murdoch, WA 6150, Australia: email: ksmith@central.murdoch.edu.au

³ Present address: Department of Biological Sciences, University of Alberta, AB, T6G 2E9, Canada.

Abstract – Individuals of *Galaxiella nigrostriata* (Shipway) from acidic, temporary, black-water wetland designated EPP 173 at Melaleuca Park, Ellen Brook, Western Australia, are compared with members from the main area of distribution of the species some 350+ km further south in Western Australia. They were found to be similar to the southern populations in size frequency distribution and habitat. Adult fish from EPP 173 were first sampled, and breed, one month later than those from southern sites. Diets of all populations were similar, comprising predominantly microcrustaceans, dipterans and rotifers; however, prey items at the water surface were consumed less commonly by the northern specimens. *G. nigrostriata* was found to be sensitive to high water temperatures. Laboratory trials showed that the fish cannot tolerate, for more than a few seconds, temperatures >26°C but preferred a temperature of 14.5°C. The survival of the *G. nigrostriata* population in EPP 173 is related to the strong thermal stratification which develops on hot days, with the surface water temperature typically reaching values >26°C but overlying cooler bottom water around 15°C which provides a cool water refuge for the resident fish population. The northern outlier population in EPP 173 occurs in the path of the urban expansion of Perth and, since it has high intrinsic conservation value, its management for conservation is paramount.

Keywords: Black-water, limnology, thermal stratification, Galaxiidae, feeding

INTRODUCTION

Galaxiella nigrostriata (Shipway, 1953) (Teleostii: Salmoniformes: Galaxiidae) is a small (maximum length ~4 cm) teleost from acidic, black-water temporary pools in the extreme southwestern corner of Australia (Figure 1). *Galaxiella nigrostriata*, *Galaxiella munda*, *Lepidogalaxias salamandroides* (Lepidogalaxiidae), and *Nannatherina balstoni* [Nannoperidae, following the current Family classification of Allen *et al.*, (2002)] are four species of freshwater teleost endemic to southwestern Australia. They have attracted scientific attention because of i) their specialised habitat within a very restricted geographic distribution, and ii) their method of surviving the seasonal drying of their habitats by aestivating in moist subsurface substrates (Christensen 1982; McDowall and Pusey 1983; Berra and Allen 1989, 1991, 1995; Leung 1988; Berra *et al.* 1989, 1990; Pusey 1989, 1990; Pusey and Stewart 1989; Pusey and Edward 1990; Jaensch 1992; Pen *et al.* 1993; Martin *et al.* 1993; Gill and

Neira 1994, Morgan *et al.* 1996, 1998). Most populations of all four species occur within a narrow strip of peat flats between Augusta and Albany, southwestern Australia, but three species have at least one outlier population (by some 350 km) north of Perth (Figure 1). Knowledge of these outlier populations is based on recent records: *G. nigrostriata* near Bunbury (Morgan *et al.* 1996, 1998) and Melaleuca Park (Knott and Jasinska 1996); *Galaxiella munda* (McDowall) (Galaxiidae) between Gingin and Muchea (Allen 1982); and *Nannatherina balstoni* (Shipway) (Khulidae) at Gingin (Morgan *et al.* 1996, 1998). The similarity of their disjunct distributions indicates that all three species may once have been more widespread in southwestern Australia.

The northern outlier population of *G. nigrostriata* occurs in an un-named wetland, designated as EPP 173 (Environmental Protection Policy Map Identification Number) (Hill *et al.* 1996)] within Melaleuca Park, some 25 km northeast of Perth,

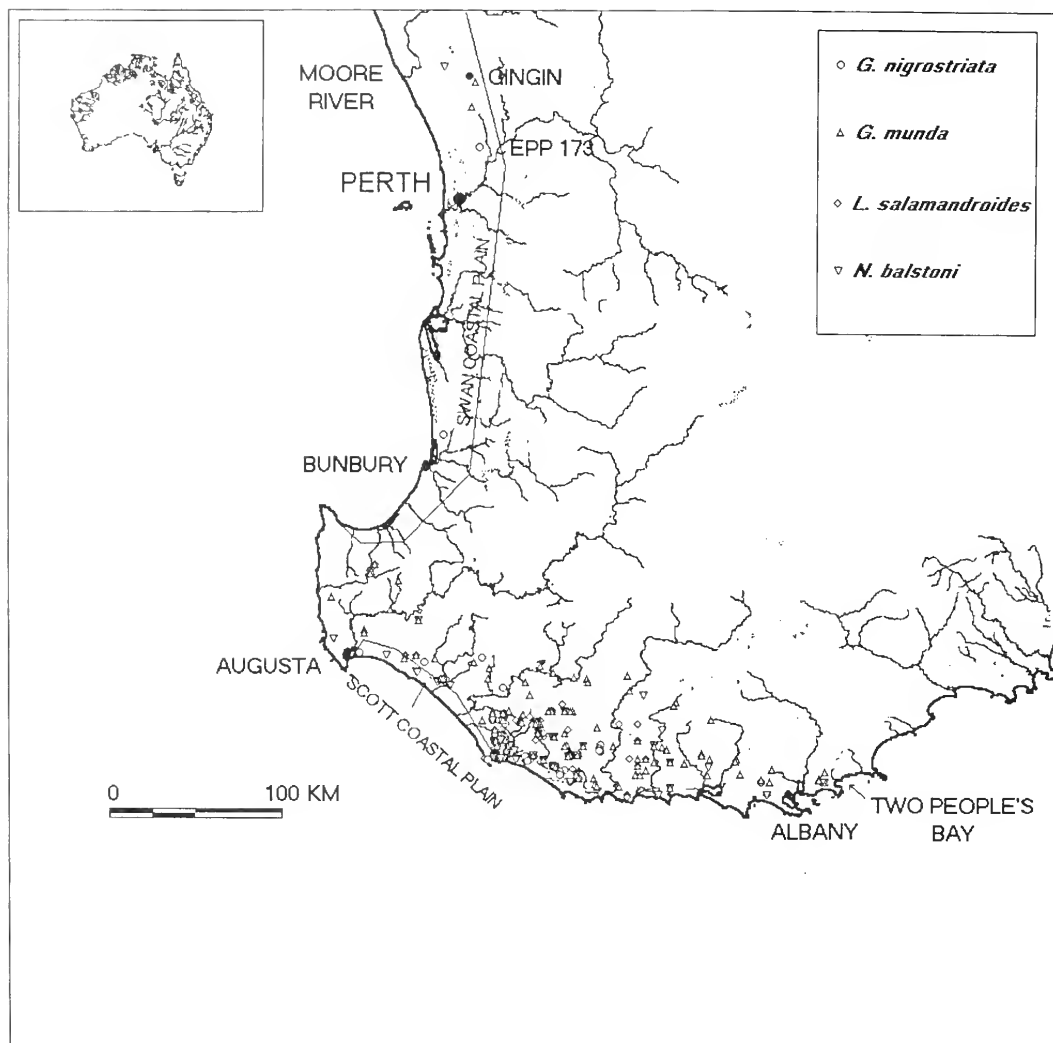


Figure 1 Distribution of *Galaxiella nigrostriata*, *Galaxiella munda*, *Lepidogalaxias salamandroides* and *Nannatherina bolstoni* within southwestern Australia.

Western Australia. Given the significantly higher day-time temperatures, particularly in summer, and lower annual rainfall at EPP 173 (31°C and 690 mm p.a., respectively) compared with the area between Augusta and Albany where *G. nigrostriata* mainly occurs (25°C and 1200 mm p.a., respectively) (meteorological data from the Bureau of Meteorology 1999), aestivation, emergence time, size structure of the population, behavioural biology and diet of *G. nigrostriata* at EPP 173, were investigated. The results are compared with published data from the southern populations (Pen *et al.* 1993; Morgan *et al.* 1996, 1998). Experimental evidence is presented supporting the hypothesis that this northern outlier population has survived

due to the specific hydrology of EPP 173. From these findings, an attempt is made to elucidate some of the factors which might limit the distribution of *G. nigrostriata*. This paper is part of a series of three concerning the outlier population of *G. nigrostriata*. In the other papers in the series, Knott *et al.* (2002) describe the unique limnological conditions in EPP 173 and Smith *et al.* (2002) describe the molecular and morphological relatedness between the outlier and southern populations.

This outlier population of *G. nigrostriata* has a strong claim for conservation, but longevity of the population is threatened from three sources: urban expansion, groundwater extraction and highway

construction. The paper concludes with an appraisal of these threats and the series contributes to knowledge of the southwest Australian piscifauna.

Study Area

The environment of EPP 173 (31°42'18"S; 115°57'41"E; elevation 50.41 m AHD (Australian Height Datum); maximum depth 70 cm; ~1.5 ha in area) is described in detail in Knott *et al.* (2002) but features salient to this paper are briefly summarised here. There is no surface drainage into EPP 173; the only other surface features are a small outflow stream to the east, and a smaller, temporary water body (Mb), contiguous with its northern margin. EPP 173 is fed *via* a permanent spring seepage which maintains an area of several square metres of boggy peat and shallow (<11 cm deep) surface water in late summer and autumn when nearby wetlands are completely dry. EPP 173 and Mb are continuous at times of peak winter levels of infilling. At EPP 173, water: salinity is low (444 mS cm⁻¹), pH decreases from 5.5 during inundation to 3.25–3.8 during the drying phase and colour is very dark (≥ 1200 TCU). Water temperatures reflect the input of cool (~15°C) ground-water, and in summer, solar heating. Surface water temperature range from ~27°C in summer to 13°C in winter (Knott *et al.* 2002). In winter, the water column is homogenous with respect to temperature but in late spring/early summer, strong thermal gradients develop, for example: 26.7°C within 2 cm of the surface to 15°C at 65 cm depth (15 November, 1995; Knott *et al.* 2002).

MATERIALS AND METHODS

Aestivation and emergence

On May 12, 1996, while the swamp was still dry, a trench (200 cm x 40 cm x 60 cm deep) straddling 2 microhabitat-types [a stand of *Baumea articulata* (Cyperaceae) and a winter open water habitat] was dug in the peat near the central area of EPP 173. The trench was filled with rainwater and the soil removed was sieved (2 mm² mesh size) to check for aestivating *G. nigrostriata*. The water-filled trench was swept with a fish net for four hours (11.00–15.00 hours) for emergent fish. Root mats in 30 cm³ blocks of soil were removed and submerged in aquaria to observe any fish emergence from that microhabitat. In late May, 1996, leaf litter, the underside of logs, as well as four blocks of sandy/peat substrate (40 cm x 40 cm x 60 cm deep) from EPP 173 were searched for aestivating fish by sieving the detritus. To record where fish aestivated and to exclude the possibility that the fish recolonised EPP 173 each year from nearby refuges, for example by swimming upstream through the

outflow channel, EPP 173 was isolated from the small auxiliary swamp, Mb, by a 30 000 x 40 cm fence of 1 mm² mesh, supported by star-pickets and inserted 10 cm into the substrate, and from the outflow stream 6 m from EPP 173 by a fence of the same mesh.

Size structure

Low numbers of animals were collected from EPP 173 to minimise the impact on the small *G. nigrostriata* population. The same individuals were used in as many aspects of the study as possible. A sample of *G. nigrostriata* large enough to construct size frequency histograms was collected on August 19 and September 19, 1996. Fish were anaesthetised in 0.015 % benzocaine solution. Total length (snout to end of tail fin) was measured using dial vernier callipers (0.1 mm increment). Only recently killed or anaesthetised fish were measured to prevent errors due to deterioration of the specimens.

Diet

Sample sizes for diet analyses are low because preserving specimens for this purpose precluded their use in other components of the study. Stomach contents were analysed as follows: numbers (+ sampling date), *ex* EPP 173: 3 adults (26 October, 1995); 12 larvae (6.7–13.3 mm) (19 August, 1996); 12 larvae and juveniles (7.08–20.72 mm) (1 October 1996); *ex* pools along Chesapeake Road, southeast of Northcliffe (34°42'S, 116°07'E): 2 adults (July, 1996); 6 (adults) (9 September, 1996). The stomach contents were identified using dissecting and compound microscopes. The diets were analysed by frequency of occurrence, describing the relative contributions of each kind of prey to the total number of prey-items within each stomach.

Laboratory experiments

Two experiments were conducted to compare the behaviour of *G. nigrostriata* from EPP 173 in aquaria with and without an established thermal gradient. Two un-aerated aquaria measuring 60 x 25.5 x 30.5 cm (length x width x depth), were filled to a depth of 28 cm with water from EPP 173 (collected in August 1996) and placed in a controlled temperature room at 17.5°C. Two treatments were established, a control and an experimental. In the control treatment, the water column was only slightly stratified with respect to temperature, 16.5°C at the bottom, varying between 17.0 and 19.5°C at the surface due to the heating effect from the light source. In the experimental treatment, a more pronounced temperature gradient was established by placing an aquarium heater (Tronic 200 Watt) horizontally and 1 cm below the water surface, whilst standing the aquarium on brick supports within an ice bath; the ice was maintained level with the bottom of the aquarium. In both, a

100 Watt light source was suspended 15 cm above the water surface to maintain constant illumination levels between treatments. Water temperature was measured using a 0–50°C E-Mill Precision thermometer (0.1°C graduated increments). In the experimental treatment, water temperatures 2 cm below the surface ranged between 24.5 and 28.0°C; water temperatures 2 cm above the bottom ranged between 8.0 and 9.5°C.

In the first experiment, fish were released individually at the surface from a net into the stratified aquarium to acclimatise for 1 hour. The position of each fish relative to the bottom of the aquarium was then recorded at three random times during the second hour. The same fish was then transferred to the control aquarium and the same procedure repeated. Eleven replicates were performed over 2 days, using a different fish in each trial. The three scores from each trial were averaged to give a mean position within the temperature gradient for each fish in each treatment. The data were analysed using a paired two-tailed t-test with 11 degrees of freedom. The second experiment compared the amount of time fish spent feeding at the surface in each temperature treatment. Collembola, which are a natural component of the diet of this species, were collected from a suburban wetland near Perth. Twelve trials were conducted using 12 different fish and the sequence of treatments to which each fish was subjected was alternated in each trial. After fish had acclimated for one hour, a 2 cm² aggregation of Collembola estimated to consist of approximately 400 animals, was added to the aquarium surface. For 15 minutes the amount of time each fish spent within 3 cm of the water surface was recorded.

RESULTS

Aestivation and emergence

In 1996, no fish were recovered in EPP 173, regardless of the search method, prior to inundation following the onset of winter rains. The first specimens in 1996, 4 adults (length, 25.5–34.0 mm), were recorded on June 29 when the water depth in the lake at the site of permanent seepage was 64 cm. On August 19, 1996, 17 *G. nigrostriata* 0+ recruits (length, 6.7–13.3 mm) and on September 19, 1996, 35 *G. nigrostriata* 0+ recruits (length, 7.0–20.7 mm) were collected from EPP 173 and also from Mb, when it was still separate from EPP 173. No *G. nigrostriata* were caught in the outflow stream downstream from the fence.

Size frequency

Seventeen specimens from EPP 173 (length, 6.7–13.3 mm) collected 19 August, 1996, and 35

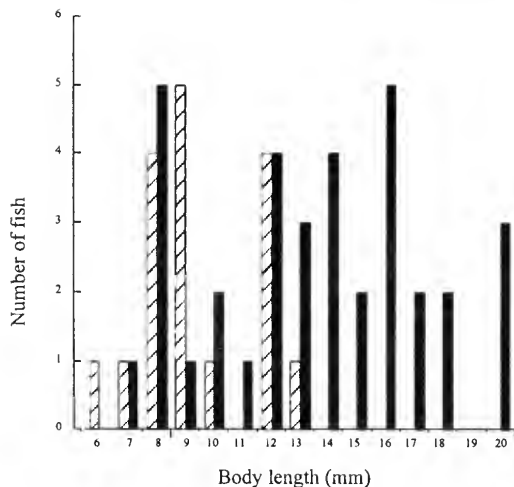


Figure 2 Length-frequency histogram of two samples of *G. nigrostriata* from EPP 173 collected in 1996. August, hatched bars; September, solid bars.

specimens (length, 7.0–20.7 mm) collected 19 September, 1996, were all 0+ recruits (Figure 2).

Diet

A total of 11 prey taxa were recorded, eight from the stomachs of specimens from EPP 173 (Figure 3) and seven from the Chesapeake Road specimens (Figure 4). Comparisons of the stomach contents

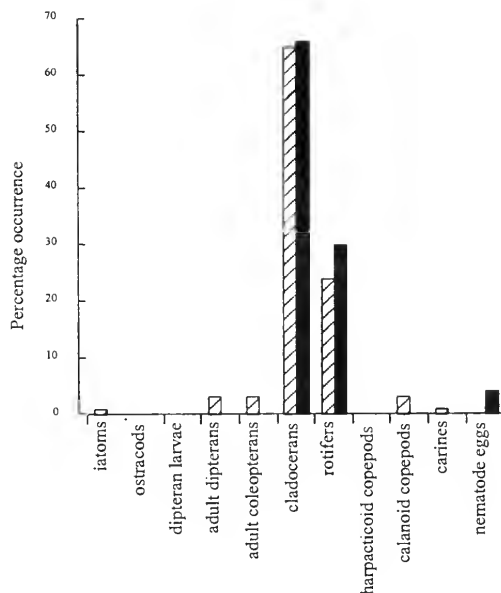


Figure 3 Combined percentage occurrence of prey taxa in stomachs of *G. nigrostriata* from EPP 173. Hatched, October 1995. Solid, August 1996.

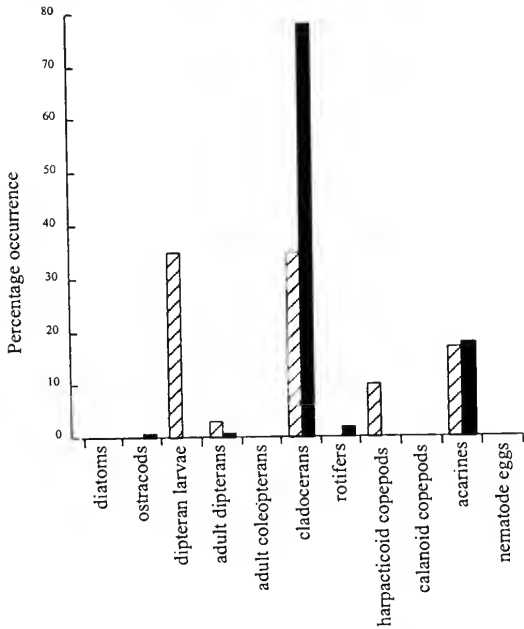


Figure 4 Combined percentage occurrence of prey taxa in *G. nigrostriata* from Chesapeake Road in the lower southwest during 1996. Hatched, July. Solid, September.

from both sites reveal no marked differences in abundance and diversity of prey consumed. Cladocerans, followed by rotifers (EPP 173) and terrestrial insects (Chesapeake Road), were the prey most commonly ingested at both sites. Harpacticoid copepods and acarines also occurred consistently in the diet of the southern fish. Other prey items, such as diatoms and calanoid copepods were recorded infrequently.

Laboratory experiments

Fish were consistently observed at greater depths in the stratified, than in the control, aquaria (Table 1).

Table 1 Average distance (cm) of *G. nigrostriata* from the bottom of the water column in stratified and unstratified (control) aquaria.

Trial	Stratified	Unstratified
1	3.7	17.5
2	3.7	8.7
3	5.7	12.3
4	4.3	7.5
5	4.3	16.7
6	4.3	7.7
7	4.5	6.7
8	2.7	16.0
9	2.5	4.8
10	2.3	14.0
11	5.7	2.7
Mean ± S.E.	4.0 ± 1.2	10.4 ± 5.1

Table 2 Time (seconds) spent feeding within 3 cm of the water surface in the stratified (S) and unstratified (C) aquaria.

Trial	First treatment	Stratified	Control
1	S	1	150
2	C	0	516
3	S	0	170
4	S	3	201
5	C	2	185
6	S	0	271
7	S	0	0
8	C	0	63
9	S	7	28
10	C	1	0
11	S	1	9
12	C	17	205
Mean ± S. E.		3 ± 5	150 ± 149

The mean position of fish in the stratified aquarium was 4.0 cm (± 1.2) from the bottom of the water column, where water temperature was 14.5°C. The average position of fish in the control aquarium, where thermal stratification was not established, was 10.4 cm (± 5.1) from the bottom at a water temperature of 17.0–18.0°C. The two results were significantly different (p = 0.003, d.f. = 10; paired two-tailed *t*-test with 11 degrees of freedom).

Similarly, fish in the control aquarium spent significantly more time feeding at the surface than did those in the stratified aquarium (Table 2). Most fish in the control aquarium frequently remained within the top 3 cm of the water column (average time 2.5 minutes), feeding constantly on prey floating at the water surface throughout the 15 minute trial period and making no attempt, subsequently, to increase their depth. In marked contrast, the fish in the stratified aquarium spent most of the time near the bottom of the water column, darting to the water surface to capture prey and then quickly returning to the bottom. The average time each fish spent within 3 cm of the water surface was less than 3 seconds, with the exception of one trial where the fish remained in the epilimnion for up to 7 seconds.

DISCUSSION

Although many wetlands of the Swan Coastal Plain have been degraded (Wrigly *et al.* 1988; Halse 1989) or lost (estimated as 70%, Halse 1989) under the impact of the European presence in Western Australia, numerous wetlands remain and 40 in the vicinity of Perth have been the subject of a major study (summarised in the seven volume series *Wetlands of the Swan Coastal Plain* edited by S. A. Balla and J. E. Davis, released during the years 1993 – 1996). The occurrence of outlier populations of three species of endemic fish known previously

only from the extreme southern area of Western Australia probably indicates that all three once had wider geographic distributions in the southwestern corner of the State. The comparatively recent discoveries of these outlier populations raise the question of how many more outlier populations may occur, even in close proximity to Perth. It is relevant, therefore, to question what limnological features may have facilitated the survival of *G. nigrostriata* within EPP 173. The main habitat of the Black-stripe minnow is temporary swamps along the coastal strip between Albany and Augusta, with the centre of distribution the peat flats along Chesapeake Road, D'Entrecasteaux National Park (Allen 1982; Morgan *et al.* 1996; Pen *et al.* 1993). The northern outlier population in EPP 173 also inhabits an acidic, black-water temporary swamp, but under markedly more stressful (lower rainfall: 690 mm p.a. compared to 1200 mm p.a.; higher summer maximum temperature averages: 31°C compared to 25°C) climatic conditions.

The presence of surface water throughout summer in EPP 173 is not a critical factor for the persistence of *G. nigrostriata* at this site, since i) no fish have been found in the permanent pool when the major part of the wetland has been dry, and ii) fish were present in Mb when it had been isolated from EPP 173 by a mesh fence. Nor is the outflow stream involved in the annual recolonisation of EPP 173 by *G. nigrostriata*. The Black-striped minnows within EPP 173 and Mb presumably aestivate within the boundaries of the swamp beds and therefore comprise a locally resident population.

Clearly acid, temporary waters are important for defining the ecophysiological niche of *G. nigrostriata*. The results presented here indicate two other features essential for the survival of this galaxiid in EPP 173: one, the input of cool (14°C) ground water; two, the high colour of the water, through which a strong temperature gradient is established during the hot days at the base of which is a refuge of cool water (Knott *et al.* 2002). Temperature stratification has also been documented for Lake Jandebup, <10 km to the west of EPP 173, but in that lake the temperature gradient does not exceed 6.6°C (Ryder and Horwitz 1995), possibly due to the water being only slightly coloured, with values between 2 to 17 g₄₄₀ m⁻¹ (Sommer and Horwitz, 1999). The extremely dark (>1200 TCU) water of EPP 173 facilitates the development of a strong thermal stratification on hot days. When Black-striped minnows are netted and lifted through the warm epilimnion, they die instantly. Consistent with this is the observation that on hot days no specimens of *G. nigrostriata* have been observed near the water surface. This stratification, with the refuge of comparatively cool bottom water is undoubtedly one of the important factors which

has enabled *G. nigrostriata* to persist in EPP 173 despite the high air temperatures.

The heat stress experiment shows that *G. nigrostriata* from EPP 173, when provided with a cool water refuge, avoid water temperatures >26°C which effectively excludes them from the surface layers. However, *G. nigrostriata* in D'Entrecasteaux National Park have been recorded in drying pools at a temperature of 34°C (Morgan *et al.* 1996, 1998). It is unclear from the available data whether there are different responses to temperature shown by the minnows from the two areas, however one might suspect *a priori* that gravid females or juveniles may be particularly susceptible to thermal stress. Thermal avoidance may also reflect scope for exercising choice: *Galaxias maculatus* avoids a plume of warm water discharged from a power station (Boubee *et al.* 1991). The predation rate on flying ants and adult Diptera, i.e. on terrestrial insects, varied seasonally in the southern populations [from 50% (in winter) to 20% (in summer) (Pen *et al.* 1993)] but there was limited predation on terrestrial insects at EPP 173 (<5% of total stomach contents). Results from the heat stress and feeding experiments indicated that the minnows can change their feeding behaviour in response to adverse temperatures at the water surface.

The effects of the warmer, dryer climate experienced at EPP 173 compared with the climate throughout the main zone of distribution of the species are evident in delays in the time of emergence of the larvae and of spawning. On July 8 1991, the predominant size class of 0+ recruits was 5 – 10 mm in the lower southwest (Pen *et al.*, 1993). In 1996, this did not become the modal size class at EPP 173 until late August. Furthermore, in September 1991, 0+ recruits ranged up to 35 mm in length in the lower southwest, but during this month in 1996 at EPP 173, no specimens larger than 20 mm were recorded. Spawning commenced in June in the southern populations in 1991 but in 1996 probably did not commence until July at EPP 173, since gravid adults were not captured there until late June. Although different years have been compared, and conclusions have been based on small sample sizes, we have not detected any evidence for biological divergence between the EPP 173 and the more southern *G. nigrostriata* populations other than the delayed emergence and subsequent spawning by adults.

We think it unlikely that EPP 173 was the only wetland of the central Swan Coastal Plain to have harboured *G. nigrostriata* until comparatively recent historical times, since dark water swamps are believed to have been well represented in wetlands of the Swan Coastal Plain before the arrival of Europeans. Now, however, these swamps occur primarily along the lower south coast. Most of the Swan Coastal Plain wetlands subjected to high

levels of disturbance are now colourless, open water systems from which *G. nigrostriata* may have been excluded by the loss of cool, bottom water refuges stemming from reduction in both colour and thermal stratification. Clearly, the population of *G. nigrostriata* at EPP 173 has high conservation status and stringent management protocols need to be established to conserve the population. Management of the groundwater supply and also of the vegetation and buffer zones surrounding the wetland will be essential.

EPP 173 is threatened from three sources. 1). The urban population in the immediate vicinity is expected to increase from 8 200 residents (1993) to 95 000 (2021+) (Department of Planning and Urban Development 1994). 2). Wetlands within Melaleuca Park are supported by seepage from the Gngangara Mound, an extensive unconfined aquifer which currently provides nearly 40% of the public water supply for Perth, a figure likely to increase to >50% over the next 15 years (Department of Conservation and Land Management 1999). Increasing groundwater abstraction has resulted in the loss of wetlands on the Swan Coastal Plain by the lowering of the water table and hydraulic heads of springs and seepages and although EPP 173 is identified as an ecologically significant wetland to be managed to an Environmental Water Requirement of 0.1 m above ground level (Water and Rivers 1997), experience suggests that it will be difficult to sustain this objective against climatic vagaries and the demand over time for water. 3). Of four alignments considered for the proposed Perth – Darwin National Highway, that most recently preferred is for construction of a highway <3 km east of EPP 173 (Department of Planning and Urban Development 1994); at present, the wetland, 100 m from the edge of Melaleuca Park gains some protection from frequent human visitation by the low intensity rural buffer further the east, with the nearest house some 440 m distant. The site will require management to preserve conditions for the water supply to be maintained, and for the water to continue stratifying on warm days, including maintenance of the vegetation buffer against wind mixing (Knott *et al.* 2002).

ACKNOWLEDGEMENTS

Sharon Stratico and Jeff Kite, Water and Rivers Commission, Western Australia played an important role in the discovery of the population of *G. nigrostriata* at Melaleuca Park; their help throughout this study is gratefully acknowledged. We also thank Gretchen Pianka for hours of assistance in the field, Luke Pen and Howard Gill for editorial comment, and Dave Morgan for compiling the map used as Figure 1. This work was supported by funding from The University of

Western Australia, and the Water and Rivers Commission, Perth.

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Genetic and morphological study of the Black-stripe minnow, *Galaxiella nigrostriata* (Salmoniformes: Galaxiidae), including a disjunct population near Perth, Western Australia

Kimberly D. Smith^{1,2}, Luke J. Pen³ and Brenton Knott¹

¹ Department of Zoology, The University of Western Australia,
35 Stirling Highway, Crawley, WA 6009, Australia

² Present address: Murdoch University Centre for Fish and Fisheries Research,
Division of Science and Engineering, School of Biological Sciences and Biotechnology,
Murdoch University, Murdoch, WA 6150, Australia: email: ksmith@central.murdoch.edu.au

³ Water and Rivers Commission, Hyatt Centre, East Perth, WA 6004, Australia

Abstract – This study was undertaken to measure the relatedness of an outlying population of Black-stripe minnow, *Galaxiella nigrostriata* (Shipway), from Melaleuca Park, 25 km northeast of Perth, to the main populations situated some 350 km to the south between Augusta and Albany. Allozyme electrophoresis was used to assess genetic divergence between populations. Univariate statistical tests were employed to compare the morphology of fish from the different locations. Reproductive isolation of *G. nigrostriata* at EPP 173 has resulted in inbreeding and reduced heterozygosity as well as differences in morphology. *Galaxiella nigrostriata* throughout its range shows unusually low levels of genetic polymorphism. One polymorphic locus was identified from the 27 loci sampled. Polymorphic individuals were restricted to the southern sites; specimens from EPP 173 were entirely monomorphic. Fish from EPP 173 had longer head lengths and shorter caudal peduncles than those in the south.

Keywords: freshwater fish, low genetic variation.

INTRODUCTION

Of the ten species of freshwater fish native to southwestern Australia, six [*Galaxias truttaceus*, *Galaxias maculatus*, *Galaxiella munda* and *Galaxiella nigrostriata* (Galaxiidae); *Lepidogalaxias salamandroides* (Lepidogalaxiidae); and *Nannatherina balstoni* (Nannopercidae)] have very restricted, coastal distributions in peat wetlands between Albany (35°02'S; 117°53'E) and Augusta (34°20'S; 115°09'E). The other four species [*Bostockia porosa* (Percichthyidae), *Edelia vittata* (Nannopercidae), *Galaxias occidentalis* (Galaxiidae), and *Tandanus bostocki* (Plotosidae)] have wider distributions between Two Peoples Bay (34°57'S; 118°11'E) and the Moore River (31°03'S; 115°35'E) (Allen 1982; Morgan *et al.* 1996, 1998). Of these ten species, eight are endemic to southwestern Australia, while *G. maculatus* and *G. truttaceus*, both with marine larval stages in some populations, also occur in Tasmania and Victoria with the geographical range of *G. maculatus* extending to New South Wales, South Australia, Queensland, New Zealand, southern South America, and the Chatham and the Falkland Islands (Allen 1982; Berra *et al.* 1996; McDowall 1996).

With the discovery in recent years of outlier populations of *G. munda* between Gingin (31°21'S; 115°54'E) and Muchea (31°35'S; 115°58'E) (Allen 1982), of *N. balstoni* at Gingin (Morgan *et al.* 1996, 1998), and of *G. nigrostriata* at Bunbury (33°19'S; 115°38'E) (Morgan *et al.* 1996, 1998) and in wetland EPP 173 in Melaleuca Park (31°42'S; 115°57'E), northeast of Perth, Western Australia (Smith *et al.* 2002) (Figure 1), there arises the question of how related are any of these widely disjunct northern populations to those from the centre of distribution of that species. The focus in this study is on the Black-stripe minnow, *Galaxiella nigrostriata* (Shipway 1953) (Teleostei: Salmoniformes: Galaxiidae). *Galaxiella nigrostriata* was originally described as a subspecies of the southeastern Australian species, *Galaxias pusillus*. Subsequently, McDowall (1978) erected the genus *Galaxiella* for the three species of diminutive galaxiids with horizontal body stripes, *G. nigrostriata*, *G. munda* and *G. pusilla*. Supplementary descriptions of *G. nigrostriata* have been provided by McDowall and Frankenberg (1981), Gill and Neira (1994), and Berra and Allen (1989) clarified the morphological differences between *G. nigrostriata* and *G. munda*.

Growth, size composition, diet and aspects of the reproductive biology of *G. nigrostriata* from the main area of distribution have been documented by Pen *et al.* (1993), while dietary studies were undertaken by Pusey and Bradshaw (1996).

The present study determined the relatedness of *G. nigrostriata* from EPP 173 to specimens from within the main area of distribution of the species. Allozyme electrophoresis was used to document genetic polymorphism and provide a basis for comparison of heterozygosity and genetic identity between sites. Morphometric analyses were used to compare the physical similarity of specimens from different geographical locations. We conclude the paper by considering the possible period of time that the northern population of *G. nigrostriata* has been isolated in EPP 173.

MATERIALS AND METHODS

Collection of Fish

Fish were collected from EPP 173 throughout the period May to September, 1996. Specimens were collected from the lower southwest between May and July, 1996; i.e. from roadside pools beside Chesapeake Road (34°42'S; 116°07'E) within the Gardner River watershed in the D'Entrecasteaux National Park and, from Scott Road near Lake Jasper (34°25'S; 115°45'E) in the Donnelly River catchment of the Shannon National Park.

Fish were collected by dragging either a pond net, diameter 85 cm, 100 mm² stretched mesh, or a 5 m wide purse seine net of 9 mm² stretched mesh through open water. Low numbers of fish were sampled in order to cause a minimum impact upon the small resident populations and consequently, where possible, specimens were used in several facets of the study.

Electrophoresis

Specimen numbers were as follows: EPP 173, 24 fish; Chesapeake Road, 16; Lake Jasper, 11. Skeletal muscle tissue was removed under a dissection microscope, homogenised with extractant (2:1, extractant: tissue by volume; extractant of 0.28 M sucrose, 0.1% (v/v) mercaptoethanol, 0.02% (w/v) bromophenol blue in 0.02 M tris, pH 8) in ceramic depression wells, using a glass test tube. The extracts were soaked onto 5 x 6 mm rectangles of chromatography paper and stored overnight at -70°C. Extracts were prepared over an ice pack on the day prior to the run to minimise deterioration of the enzymes.

Gels contained between 18 and 19.5 g of hydrolysed potato starch (Starch Art) and approximately 165 mL of the appropriate buffer solution. Starch gels were prepared 24 hours prior to runs which were made at varying voltages and

currents, for different periods of time according to the requirements of each buffer solution. Staining for enzymes followed the protocols described in Richardson *et al.* (1986). For loci encoding enzymes exhibiting polymorphisms, data were collected running a maximum of 14 individuals from a site on a gel together with a minimum of two individuals of known genotype from an alternative location.

Allelic frequencies at the polymorphic locus were calculated and estimates of heterozygosity obtained according to the method of Nevo (1978). Nei's index of genetic identity was calculated to quantify the similarity between the samples (Nei 1978).

Morphometric Analyses

Sample sizes were as follows: EPP 173, 11; Lake Jasper, 16; Chesapeake Road, 36. Eight measurable characters were assessed for each fish using a dissecting microscope: total length (snout to posterior margin of tail = TL), head length (HL), eye diameter (ED), body depth (BD), eye to snout length (E-S), caudal depth (CD), caudal length (CL), length of base of anal fin (FL) and four countable ray numbers (in the pectoral, anal, dorsal and tail fins).

To eliminate the risk of errors due to preservation artefacts only very recently dead and/or anaesthetised fish were used for analysis. In order to determine the effect of sex on character variation, specimens from the Lake Jasper site were humanely killed by an overdose of anaesthetic, dissected and their sex identified by the presence of ovary or testis within the body cavity. Each character was tested for sexual dimorphism using an unpaired 2-tailed *t*-test. With the exception of body depth (BD), each character was independent of sex (95% confidence interval). Given the limited number of specimens available, and the need to use them in a number of aspects of this study, BD was eliminated from the analyses, with the remaining analyses conducted independent of sex. Fish were not sufficiently abundant to permit the comparison of only similar-sized specimens. Linear regression analyses were performed using the Chesapeake Road sample to test whether the relationship of each measurable character to total length was isometric; all characters increased linearly with body size enabling different sized specimens to be compared by standardising character values. Measurable characters were standardised by dividing them by body length of the specimen. All specimens were longer than 13.2 mm standard length, the length by which all fin rays are formed (Gill and Neira 1994). Levene's homogeneity of variance test was applied to qualify the assumption that means for each character were normally distributed within samples. One-way analyses of variance were calculated between sites for each of the meristic and standardised measurable characters.

Table 1 Proteins showing resolvable banding in *G. nigrostriata* and buffer systems giving best resolution.

Protein	Buffer type	No. Loci	Variability
Adenosine deaminase	TEB	1	M
Adenylate kinase	TC8	2	M
Alcohol dehydrogenase	TM	1	M
Creatine kinase	TC8	2	M
αEsterase	TM	1	M
βEsterase	TM	2	M
Glucose 6-phosphate dehydrogenase	TEB	1	M
α-Glycerophosphate dehydrogenase	TEB	2	M
Isocitrate dehydrogenase	TC8	1	M
Lactate dehydrogenase	TM	2	M
Leucine aminopeptidase	TEB	1	M
Malate dehydrogenase	TM	2	1M, 1P
Peptidases			
L-Leucyl-glycylglycine	TM	1	M
L-Leucyl-Proline	TM	1	M
L-Leucyl-L-Tyrosine	TM	1	M
L-Valyl-Leucine	TEB	1	M
6-Phosphogluconate dehydrogenase	TEB	1	M
Phosphoglucose isomerase	TEB	1	M
Phosphoglucomutase	TEB	1	M
Superoxide dismutase	A	2	M

RESULTS

Electrophoresis

Polymorphism was very low; of the 27 loci encoding 20 enzymes clearly resolvable, just one polymorphism was identified (Table 1) – malate dehydrogenase exhibited 3-banded dimeric variants for two alleles. The level of polymorphism recorded for *G. nigrostriata* from both sites within its main area of distribution was 3%; the EPP 173 specimens were entirely monomorphic (Table 2). An additional 11 enzymes assayed showed unresolvable banding patterns and remained ambiguous despite repeated efforts combining liver and muscle tissue, using alternative buffers and increasing the concentration of the stain twofold.

Heterozygote frequencies of Mdh at the Chesapeake Road and Lake Jasper sites fitted frequencies expected under Hardy-Weinberg equilibrium ($p > 0.01$). There were significant differences in allele frequencies at the polymorphic locus between all sites ($p < 0.05$). Average overall heterozygosity at Chesapeake Road and Lake Jasper was 0.018 and 0.008 respectively. Nil heterozygosity was recorded at EPP 173. The values obtained for

Table 2 Allele frequencies at the malate dehydrogenase locus; the only locus found to be polymorphic in Black-stripe minnow.

Collection site	Sample size	“Slow”	“Fast”
Melaleuca Park	24	1	0
Chesapeake Road	16	0.125	0.875
Lake Jasper	11	0.5	0.5

Table 3 Between-site comparisons of Nei’s genetic similarity (I).

Comparison	I
Chesapeake Road versus Lake Jasper	.996
Chesapeake Road versus EPP 173	.999
Lake Jasper versus EPP 173	.997

Nei’s (1978) similarity indices were very close to the theoretical maximum value of one between all sites (Table 3).

Morphometric analyses

The values of each measurable character increased linearly with increasing total body length; correlation co-efficients were very close to one (Table 4). Standardised head lengths within the EPP 173 population (mean 19.6% B.L.) were found to be significantly larger ($p = 0.02$) than those from fish collected near Lake Jasper (mean 18.5% B.L.) (Table 5). Similarly, standardised caudal peduncle lengths were shorter at EPP 173

Table 4 Correlation co-efficients of linear regression analyses defining the relationship between each measurable character and total body length.

Character	Correlation co-efficient
Head length	$r = 0.952$
Eye diameter	$r = 0.763$
Eye-nose distance	$r = 0.870$
Caudal depth	$r = 0.669$
Caudal length	$r = 0.860$

Table 5 Range and mean (\pm standard deviation) of morphological characters used to compare *G. nigrostriata* from three locations.

	EPP 173 n = 11		Lake Jasper N = 16		Chesapeake Road N = 35	
TL (mm)	20.9 – 34.0	(28.4 \pm 4.7)	25.9 – 35.8	(30.6 \pm 2.9)	17.8 – 43.0	(32.4 \pm 5.6)
HL (% BL)	17.7 – 21.3	(19.6 \pm 0.99)	16.7 – 20.8	(18.5 \pm 1.07)	15.9 – 21.2	(18.8 \pm 1.04)
ED(% BL)	4.8 – 6.8	(6.0 \pm 0.56)	4.7 – 6.1	(5.5 \pm 0.40)	4.7 – 8.1	(5.9 \pm 0.70)
E–N(% BL)	3.6 – 5.2	(4.4 \pm 0.53)	3.5 – 5.0	(4.2 \pm 0.46)	2.9 – 5.9	(4.3 \pm 0.51)
CD(% BL)	4.8 – 5.5	(5.1 \pm 0.30)	3.8 – 6.1	(4.9 \pm 0.52)	2.4 – 9.4	(4.9 \pm 0.96)
CL(% BL)	14.1 – 16.8	(16.0 \pm 0.80)	15.5 – 18.9	(16.8 \pm 0.99)	14.4 – 24.9	(17.4 \pm 1.75)
Pectoral fins	11 – 13	12 \pm 1.0	11 – 13	11.9 \pm 0.5	10 – 13	12 \pm 0.6
Anal fins	7 – 10	(9.3 \pm 0.9)	9 – 10	(9.5 \pm 0.5)	7 – 10	(9.4 \pm 1.0)
Dorsal fins	7 – 8	(7.4 \pm 0.5)	5 – 7	(6.4 \pm 0.7)	5 – 8	(6.8 \pm 0.8)
Tail fins	14 – 15	(14.5 \pm 0.5)	14 – 15	(14.2 \pm 0.4)	14 – 15	(14.1 \pm 0.3)

(mean 16% B.L.) compared with the Chesapeake Road (mean 17.4% B.L.) ($p = 0.02$).

DISCUSSION

Galaxiella nigrostriata recorded approximately 3% polymorphism; of 27 loci assayed, only one was polymorphic. This value, compared to values between 15 and 20% commonly recorded from vertebrates, is very low (Nevo 1978). For example, Watts *et al.* (1995), recorded 20% of loci polymorphic in *G. occidentalis*, a relatively widespread galaxiid endemic to southwestern Australia. While genetic similarity between fish from the three different locations sampled is very high and does not reflect geographic distance, the northern population, in contrast to the main population is entirely monomorphic, indicating that reproductive isolation and small population size at EPP 173 has possibly resulted in inbreeding effects. Furthermore, while differences in two morphological characters were not consistent between EPP 173 specimens and those from the southern locations, the fact that there were no differences between fish collected from within the main southern area of distribution indicates that isolation at EPP 173 is influencing the appearance of the fish.

These small differences which have arisen between the EPP 173 population of *G. nigrostriata* and the main populations indicate that the population at EPP 173 has been reproductively isolated for enough generations for genetic and morphological divergence to occur. Since wide-scale urban and rural development of the Swan Coastal Plain, and the subsequent alteration of intervening wetlands commenced early this century (Bekle and Gentili 1966; Seddon 1972; Wrigley *et al.* 1988; Halse 1989), *G. nigrostriata* at EPP 173 is likely to have been isolated for at least several decades. We conclude that the population of *G. nigrostriata* at EPP 173 is not the result of recent colonisation, but is a long established population which has persisted there presumably

because this wetland has not been subject yet to significant degradation.

Given the rapid (one year) life cycle of this species (Pen *et al.* 1993), and the likelihood that the population at EPP 173 has been isolated for several decades, it is surprising that genetic differentiation is not more pronounced. For example, the *Galaxias* genotype has been shown capable of quite rapid evolution as a result of landlocking behind hydro-electric impoundments (Fulton 1978) and segregation in different river systems (Watts *et al.* 1995). Indeed, small levels of environmental heterogeneity were regarded by Wallis *et al.*, (2001) to be a sufficient reason explaining genetic divergence in populations of *Galaxias vulgaris* Stokell in the South Island of New Zealand. However, in *G. nigrostriata*, genetic divergence appears to have been limited by low levels of genetic variation within the genome of this species.

There are several possible explanations for the peculiarly low levels of genetic polymorphism detected across the range of *G. nigrostriata*, and subsequently for the absence of pronounced genetic divergence between populations. Although *G. nigrostriata* can occur on two widely separated geomorphic units (namely the Swan and Scott Coastal Plains), it is known only from waters with a narrow range of physical and chemical conditions (Smith *et al.* 2002; Knott *et al.* 2002). Although such ephemeral, acidic (pH 3.25–5.5) black-water (colour >1200 TCU) habitats may embody physiologically extreme conditions in comparison with other Australian freshwater habitats, they probably are reasonably constant in their physical and chemical conditions. The narrow range of environmental conditions (i.e. uniform habitat) occupied by *G. nigrostriata* may have caused directional selection for homozygosity and the fixation of a small range of genotypes. The resulting lack of heterozygosity may have subsequently reduced the ability of this species to adapt to the rapid environmental changes to wetland habitats induced by Europeans this century.

Low levels of genetic variation are likely to reflect the degree to which habitat alteration has reduced the number of *G. nigrostriata* populations on the Swan Coastal Plain, causing inbreeding. Several northern outlier populations of freshwater fishes mainly from the lower south west indicate that stocks remaining at EPP 173 and within the narrow strip of southwest coastal peat flats represent only a minor proportion of the original population size. The absence of heterozygotes at EPP 173 indicates the vulnerability of this species to inbreeding. Heterozygosity within the polymorphic locus of fish from within the main population does not indicate inbreeding; inter-breeding is possibly facilitated by extensive seasonal flooding which causes large wetland areas along the south coast to become connected. Within this main population, however, overall heterozygosity is unusually low and is comparable to that of fishes which have had histories of population depletion.

Low levels of genetic polymorphism (6%) and overall heterozygosity (0.013) have also been detected in the North American paddlefish, *Polydon spathula* (Carlson *et al.* 1982). *P. spathula*, like *G. nigrostriata*, occurs in a very narrow range of environmental conditions and has been significantly adversely affected by habitat alteration and is now absent from major areas of its original range (Carlson *et al.* 1982). The low (4%) level of polymorphism of *Sardinella aurita*, abundant throughout the Mediterranean and off Western Africa, (Chikhi *et al.* 1998), has been attributed to a combination of collapses in fish stocks caused by over fishing, variations in reproductive success and possibly mass extinctions caused by ancient glaciation cycles.

The northern population of *G. nigrostriata* could have been established in comparatively recent times, explaining the lack of genetic divergence from the main population. Colonisation could have been facilitated *via* a spring-fed stream which during winter and early spring connects EPP 173 with Ellen Brook, a tributary of the Swan River. However, the nearest documented population of *G. nigrostriata* is over 200 km away at Bunbury, and the wetland harbouring this population is widely separated from the Swan River catchment.

However, the present distribution pattern of the endemic fish fauna, and particularly the disjunct patterns of three species with northern outlier populations [*G. nigrostriata* at EPP 173, *G. munda* (Allen 1982) and *N. balstoni* (Morgan *et al.* 1998) near Gingin] and with specialised breeding requirements (acid, black, temporary water), suggests that previously species had a wider distribution through the southwest corner of Australia, particularly along the Swan Coastal Plain. The presence of Europeans has had a markedly deleterious impact, with extensive urban

and rural developments leading to alteration of intervening wetlands. Consequently, the population of *G. nigrostriata* at EPP 173 may be of long-standing but it is impossible as yet to estimate the length of the period of complete isolation – likely to have been several decades, at least. At least one species of invertebrate, *Rak obtusus* (Cladocera), also an inhabitant of EPP 173, is otherwise only recorded from wetlands in the lower southwest; further descriptions of aquatic invertebrates from the wetlands at Melaleuca Park could reveal more relictual faunae. More detailed genetic studies, involving DNA assays and comparisons between the other endemic freshwater fishes, some with outlying populations, are essential to provide additional insight into the effects of wetland alteration upon the freshwater piscine fauna in Western Australia.

ACKNOWLEDGEMENTS

We gratefully acknowledge the assistance of: Jeff Kite and Sharon Stratico, Water and Rivers Commission, Perth, who provided strong support for studies on EPP 173; Howard Gill and Dave Morgan, Murdoch University, Perth, for providing specimens as well as data from their research into the distributions of freshwater fish in south-western Australia.

Funding from both the Department of Zoology, The University of Western Australia, and the Water and Rivers Commission, Perth, is also gratefully acknowledged.

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Limnology and aquatic fauna of EPP 173, Melaleuca Park, refuge for an outlier population of the Black-stripe minnow *Galaxiella nigrostriata* (Galaxiidae), in southwestern Australia

Brenton Knott¹, Edyta J. Jasinska^{1,2} and Kimberly D. Smith^{1,3}

¹ Department of Zoology, The University of Western Australia,
35 Stirling Highway, Crawley, WA, 6009, Australia: email: bknot@cylle.uwa.edu.au

² Present address: Department of Biological Sciences, University of Alberta,
AB, T6G 2E9, Canada: email: edytaj@ualberta.ca

³ Present address: Murdoch University Centre for Fish and Fisheries Research,
Division of Science and Engineering, School of Biological Sciences and Biotechnology,
Murdoch University, Murdoch, WA 6150, Australia: email: ksmith@central.murdoch.edu.au

Abstract – The physicochemistry, hydrology and invertebrate fauna are described for an unusual wetland, EPP 173, in Melaleuca Park, near Perth, Western Australia. EPP 173 is important as the site for a northern outlier population of the Black-stripe minnow, *Galaxiella nigrostriata* (Shipway), a fish endemic to southwestern Australia. EPP 173 is an acid (pH <5.5, typically pH 3.3 to 3.9), seasonal wetland with unusually dark water (TCU >1200). The colour of the water together with the surrounding forest and wetland vegetation facilitate the establishment and persistence of strong thermal stratification of the wetland in spring and summer. The invertebrate fauna comprises 41 species with a substantial benthic cladoceran component, including at least one species previously known only from southern wetlands between Augusta and Albany. The wetland is of high conservation value, containing no exotic species and low concentrations of nutrients – accompanied by the absence of algal blooms. However, encroaching urban development is likely to alter the limnology of EPP 173, threatening the survival of the resident *G. nigrostriata* population.

Extra keywords: thermal stratification, disjunct distributions, aestivating fish, refugia, aquatic invertebrates.

INTRODUCTION

Galaxiella nigrostriata (Shipway, 1953), *G. munda* McDowall, 1978 (Galaxiidae), *Lepidogalaxias salmandroides* Mees, 1961 (Lepidogalaxiidae), and *Nannatherina balstoni* Regan, 1906 (Nannoperidae) are freshwater teleosts endemic to Western Australia, occurring in temporary, acidic, dark-water wetlands on peat flats between Augusta and Albany in the southwest of the State. Of these four species, three are also known from outlier populations north of their main area of distribution: *G. nigrostriata*, at Bunbury (Morgan *et al.* 1996, 1998) and EPP 173 in Melaleuca Park (Smith *et al.* 2002a; 2002b); *G. munda*, between Gingin and Muchea (Allen 1982, Morgan *et al.* 1996, 1998), and *N. balstoni* at Gingin (Morgan *et al.* 1996, 1998). There is remarkably little biological divergence between the outlier and southern populations of *G. nigrostriata*, which are separated by a distance of 350 km (Smith *et al.* 2002a), while slight differences have arisen in morphology and genetics (Smith *et al.* (2002b).

The northern outlier population of *G. nigrostriata* occurs in wetland EPP 173 within Melaleuca Park (Figure 1), northeast of Perth. Although the aquatic environments throughout the Black-stripe minnow's distribution are similar, namely acidic, black-water, temporary swamps, the northern population experiences a warmer and more arid climate. Smith *et al.* (2002a) demonstrated that cool, bottom-water refugia provided by strong thermal stratification of the dark waters in EPP 173 enable the continuing survival of the northernmost population of *G. nigrostriata*. The purpose of this paper is to describe the limnology and setting of EPP 173 to help explain the presence of the northern most outlier population of *G. nigrostriata* at EPP 173 and to provide the environmental context for the biological (Smith *et al.* 2002a) and morphogenetic (Smith *et al.* 2002b) comparisons between the southern and outlier populations.

Study Area

Melaleuca Park covers approximately 3000 ha of

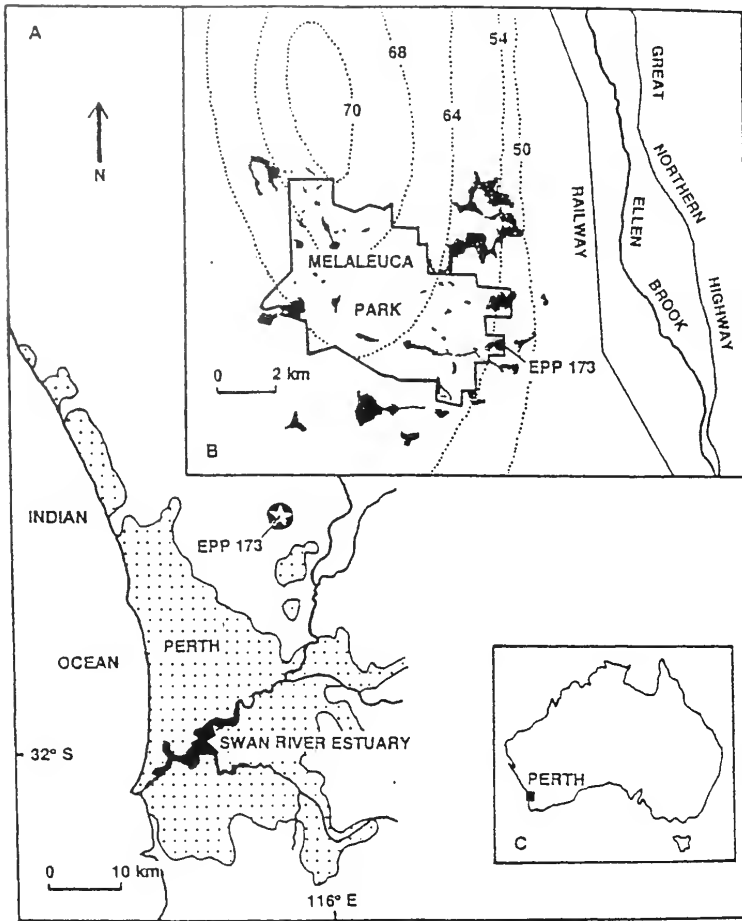


Figure 1 Map showing the location of: Melaleuca Park (A); EPP 173 on the eastern boundary of Melaleuca Park (B); and (C), the general location of map 1A. A: centre of the star marks the location of EPP 173; stippling indicates urban areas; also shown are major lines of drainage lines into the Swan River estuary. B: dotted lines indicate water-table contours of the Gangara Mound, values in m Australian Height Datum; coarse stippling indicates wetlands in and near Melaleuca Park.

uncleared Crown Land (Department of Conservation and Environment 1983). It is situated on the siliceous sands of the Bassendean Dune geomorphic unit of the Swan Coastal Plain. The Park (Figure 1) lies within the eastern discharge area of the southern section of the Gngara Mound, a complex of unconfined aquifers between the Swan and Moore Rivers (Davidson 1995). Melaleuca Park contains numerous wetlands disturbed, to varying degrees, by fire and/or human activity: a general description of the Park is given in Environmental Protection Authority (1998: Volume 2B, pp 146–148). The wetland harbouring *G. nigrostriata*, EPP 173 [un-named but number designated by Hill *et al* (1996)], is one of a complex of four swamps located on the eastern boundary of

the Park: 31°42'22"S , 115°57'48"E (MK 016919) (Muchea Sheet, 2034-I SE, Australian 1:25 000 Topographical Survey); elevation 50.41 m AHD (Australian Height Datum); area ~1.5 ha. The complex of four swamps appear, from aerial photographs, to be remnants of one, large ancestral swamp. On the northern perimeter of EPP 173 is a small wetland, designated here "Mb", continuous with EPP 173 at high water levels. There is no surface drainage in the area other than a seasonal outflow creek from EPP 173. Of the four wetlands, EPP 173 alone receives a permanent groundwater discharge. This spring seepage, on the western side of the wetland, maintains an area of several square metres of standing water (<11cm) over boggy peat overgrown with *Baumea articulata* (Cyperaceae), in

late summer and autumn when the remainder of the wetland and the others nearby dry out completely. Springs are a common form of groundwater discharge from the eastern flanks of the Gngangara Mound where the highly porous Bassendean sands interdigitate with clays. The sediment profile in the centre of the wetland comprises a highly compacted superficial layer (7 cm deep) of fine organic peat; underlain by a mixture of sand and peat, with the peat content declining to 20 cm depth where it is replaced by coarse white sand with little or no organic material.

The climate is markedly seasonal, with hot summers and cool moist winters. Average day-time temperatures at Melaleuca Park are 31°C in summer and 18°C during winter. Average rainfall over the Gngangara Mound is 800 mm p.a. with <5% falling in summer (Bureau of Meteorology, Perth, 1999). Average Class A pan evaporation of 1819 mm p.a. substantially exceeds the annual rainfall (Davis and Rolls 1987), but maximum evaporation rates occur when the wetland is dry except for the small area of standing water about the spring discharge. About Perth, droughts can last up to six months at a time (Newsome and Pickett 1993).

The surrounding vegetation of EPP 173 is dominated by open *Banksia menziesii* R. Br. woodland with low scattered marri (*Corymbia calophylla* R.Br.) and jarrah (*Eucalyptus marginata* Sm.) grading into a line of paperbark (*Melaleuca preissiana* Schau) around part of the margin of the wetland. Shore-parallel vegetation zones are most obvious along the eastern side of the swamp where the edge of the wetland is most clearly defined. Starting at the swamp edge, *Leptocarpus* sp. 1 (Restionaceae) grades into a mixed stand of the woody shrub *Astartea fascicularis* (Labill.) DC. and *Leptocarpus* sp. 2 with scattered specimens of another woody shrub, *Calothamnus lateralis* Lindley; the next band of vegetation the sedge *Lepidosperma longitudinale* Labill. (Cyperaceae) is separated by an area of open water from the central zone of the jointed twig-rush, *Baumea articulata* (R.Br. S.T. Blake) (Cyperaceae) which covers 0.7 ha or 47% of the total swamp area. The growth of *L. longitudinale* on columns >21 cm high ('fire columns') indicates that at least part of the swamp has been burnt, and fire edges crossing the area of *B. articulata* are evident in aerial photographs. Western Australian Department of Conservation and Land Management (CALM) unpublished fire records show that the eastern sector of Melaleuca Park has been burnt twice since 1950.

MATERIALS AND METHODS

EPP 173 was sampled on nine occasions, commencing 4 November, 1995. Water temperature and conductivity profiles were measured on 15

November, 1995, and 17 November, 1997, at two sites: site 1 – open water; site 2 – *Baumea* stand. An additional electrical conductivity profile was measured at site 1 on 16 December, 1998. Dissolved oxygen profiles were measured at the same two sites on 17 November, 1997. Dates of other water quality measurements taken at a single depth (10 cm) are presented together with the data. The limnological parameters measured: water temperature using variously ORION Model 140 Conductivity and Salinity, or LF 95 WTW Conductivity, meters or immersing Hg thermometer with 0.1°C divisions; conductivity using a LF 95 WTW Conductivity Meter, dissolved oxygen using a Microprocessor Oximeter WTW OX 196; and pH using a LC80A meter.

Water samples were analysed for colour, N-NO_3^- , N-NO_2^- , N-NH_4^+ , P-PO_4^{3-} , Na^+ , K^+ , Ca^{2+} , Mg^{2+} , SO_4^{2-} , Cl^- and $\text{HCO}_3^-/\text{CO}_3^{2-}$ by the Chemistry Centre (Western Australia).

Invertebrate fauna was sampled by 1-minute-long sweeps with a 1 mm² mesh net (25 cm x 25 cm frame). Four microhabitats – the outflow creek, central *Baumea* stand, more peripheral reeds (*Lepidosperma*) and ti-tree (*Astartea*) – were sampled on 4 November, 1995, and 17 November, 1997. Fauna samples were sorted live in the laboratory using dissecting microscope then preserved in 70% ethanol.

RESULTS

Limnology

During April–September, 1996 (late autumn to winter), no thermal stratification developed in EPP 173. Mid-day surface water temperatures of the open water during this coolest and wettest part of the year ranged from 12.8°C to 17.0°C (average = 14.4 ± 1.3 SD). With the onset of warm days, such as 24.6°C (early afternoon air temperature) on November 15 (1995) and 27.2°C on November 17, 1997, a steep temperature gradient developed within the water column (Figure 2). The greatest drop in temperature, of 8.8°C, occurred in the uppermost 10 cm of the water column (Figure 2). The bottom waters (>20 cm depth) generally remained at around 15°C (Figure 2).

Electrical conductivity profiles varied but not consistently with variations in depth even when temperature gradients had developed. There was a slight increase from 360 to 380 mS/cm with depth on 15 November, 1995 (Figure 3). However, conductivity values decreased from 500 mS/cm (surface) to 397 mS/cm (bottom) on 17 November, 1997. On the 16 December temperature decreased from 26°C at the surface to 20°C at the bottom (40 cm), conductivity, however, was constant and slightly higher than 500 mS/cm (Figure 3).

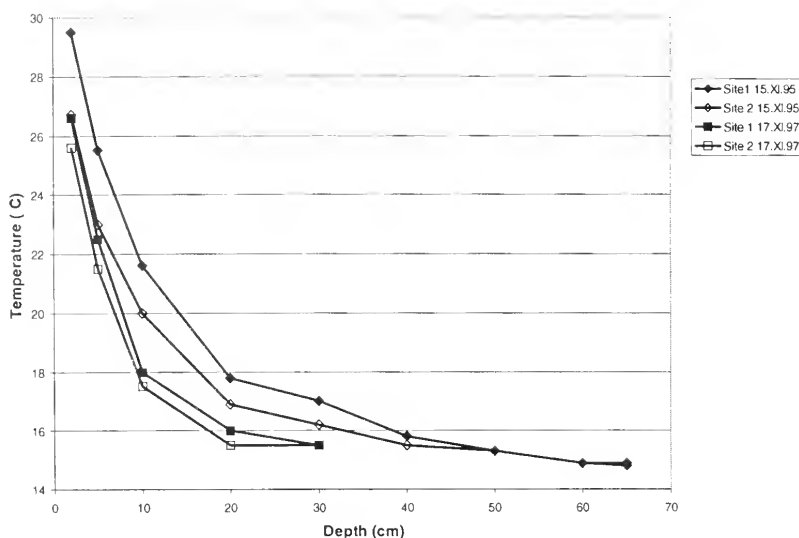


Figure 2 Temperature profile in EPP 173 in November 1995 and 1997. Each temperature and conductivity profile was taken from the water surface to the bottom of the water column – the different lengths for each curve representing different depths of each sampling site within the wetland. Upper four curves represent conductivity while water temperature is shown by the lower four curves.

Dissolved oxygen profiles were measured on 17 November, 1997, at the same sites as the temperature profiles. The DO gradient reflected that of temperature. Oxygen saturation was: highest at 70 to 80% (5.5 to 6.75 mg/L) in the uppermost 10 cm; between 50 to 60% (through the depths 10–30 cm; and around 40% (4.4 mg/L) at the bottom (28 cm depth).

EPP 173 was highly acidic, usually pH 3.3 – pH 3.9 except following episodes of heavy rainfall as in August, 1996, and December, 1998, when it had risen above pH 5 (Figure 3). On every sampling occasion, pH was uniform through the water column.

Ionic composition of the water (Table 1) reflects seawater ionic dominance, and little departure from

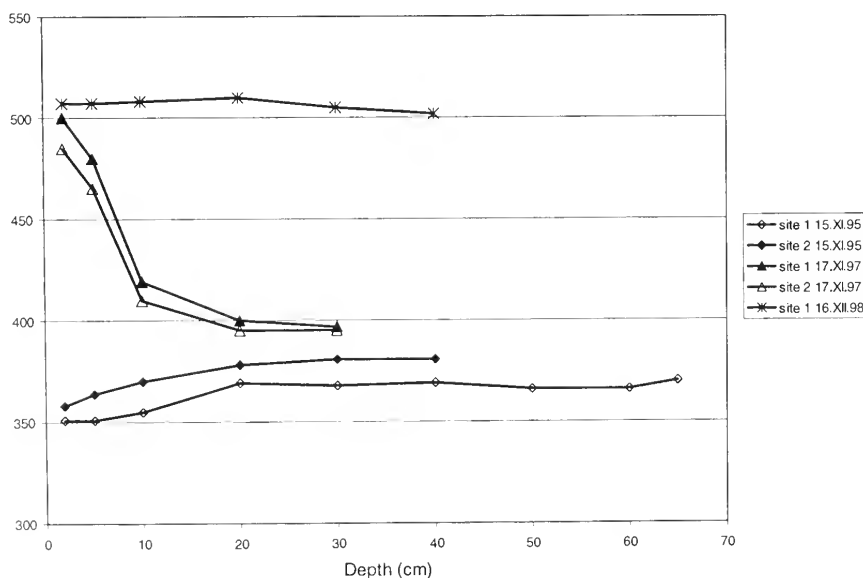


Figure 3 Electrical conductivity profiles in EPP 173 between November 1995 and December 1998.

Table 1 Ionic dominance series (mEq%) for EPP 173 (averages \pm SD of data collected on 17 Oct '97, 27 Nov '97 and 16 Dec '98) and for sea water.

	Na ⁺	Anions Mg ²⁺	Ca ²⁺	K ⁺
EPP 173	78 \pm 13.9	17 \pm 1.7	3 \pm 0.6	2 \pm 1.2
Sea water*	77	17.6	3.3	1.6
	Cations			
	Cl ⁻	SO ₄ ²⁻	CO ₃ ²⁻ + HCO ₃ ⁻	
EPP 173	91.2 \pm 10.4	8.0 \pm 0	0.8 \pm 0	
Sea water*	90.4	9.3	0.3	

*Bayly and Williams, 1973

seawater milli-equivalent proportions. However, unlike seawater, due to the much lower concentrations of ions in the freshwater EPP 173, the resulting final concentrations of CO₃²⁻/HCO₃⁻ were very low indicating a correspondingly low buffering capacity.

EPP 173 water was exceptionally dark, with ³1200 TCU at times late in the year [for example on 4 November, 1995 (when the Secchi disc depth was 13 cm, of a total water depth of 65 cm)], 17 October, 1997, and 16 December, 1998). However, early in

the year immediately following inundation the water on one occasion was noted (but not measured) to be scarcely coloured.

Phosphorus levels were low in EPP 173: total phosphorus 0.03 mg/L, phosphate 0.02 mg/L. Nitrogen concentrations were: ammonium 0.21 mg/L, nitrate < 0.02 mg/L and total nitrogen 2.3 mg/L. Chlorophyll levels were very low: chlorophyll 'a' < 0.001 mg/L, chlorophyll 'b' = 0.003 mg/L, chlorophyll 'c' = 0.004 mg/L, phaeophytin = 0.012 mg/L.

Invertebrate fauna

In all, 41 species of invertebrates were recorded from EPP 173 (Table 2). The most abundant and diverse subset of the fauna were the cladocerans which comprised nine of the 41 species. Eight of the cladocerans were benthic dwelling species (Macrothricidae and Chydoridae). The most species-rich habitats were submerged ti-tree (*Astartea fascicularis*) and the reeds (*Lepidosperma longitudinale*) while the central *Baumea* stand had the lowest number of species. The late-summer pool about the spring outflow harbours odonatan nymphs but is not utilised by the minnow (*Smith et al.* 2002a).

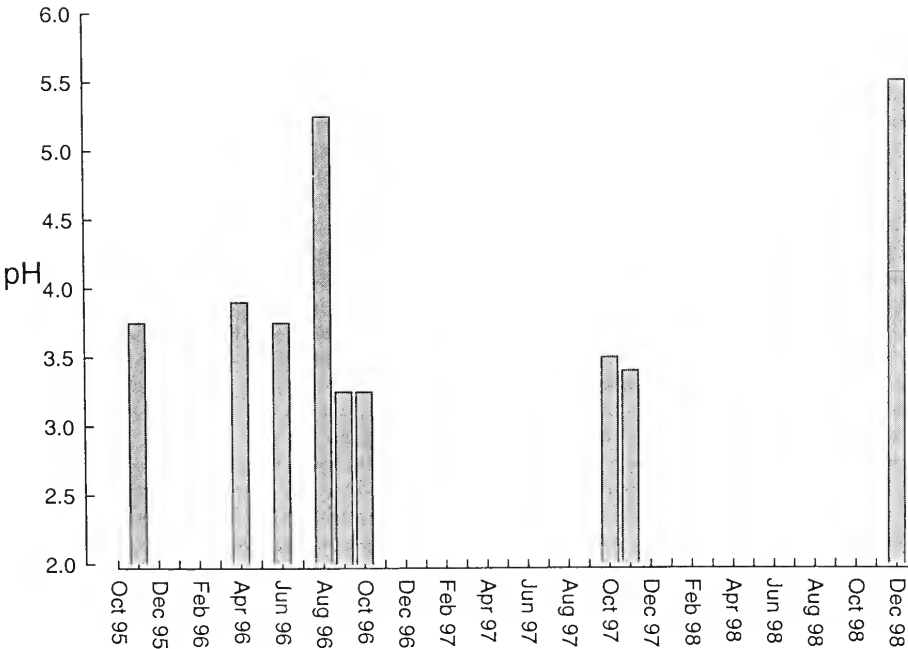


Figure 4 pH values of EPP 173 water, 1995 to 1998.

Table 2 Invertebrate fauna collected from EPP 173 in the springs of 1995 and 1997.

Taxa	Baumea	ti-tree	reeds	creek	Total # of occurrences
CRUSTACEA					
Cladocera					
<i>Ilyocryptus</i> sp. 1					
<i>Scapholeberis kingi</i> (Sars 1903)			1		1
<i>Alonella clathratula</i> Sars 1888	1		1	1	3
<i>Biapertura setigera</i> (Brehm 1931)	1		1		2
<i>Biapertura rigidicaudis</i> (Smirnov 1971)	1	1	1		3
<i>Graptoleberis testudinaria</i> (Fischer 1848)	1	1	1	1	4
<i>Monope reticulata</i> (Henry 1922)	1				1
<i>Rak obtusus</i> (Smirnov and Timms 1983)	1	1	1		3
? gen. nov. (closest to <i>Rhynchochydorus</i>)		1	1		2
Copepoda		1			1
<i>Calanoccia tasmanica</i> (Smith 1909)					
<i>Mesocyclops</i> sp. 1	1	1	1		3
<i>Paracyclops</i> sp. 1		1	1	1	3
Ostracoda	1	1	1	1	4
<i>Ilyodromus</i> sp. 1					
Decapoda		1	1		2
<i>Cherax quinquecarinatus</i> (Gray, 1845)					
INSECTA	1	1	1	1	3
Diptera					
<i>Chaoborinae</i> sp. 1					
<i>Alotanypus dalyupensis</i> (Freeman 1961)				1	1
<i>Harrisius</i> sp. 1				1	1
<i>Limnophyes pullulus</i> (Skuse 1989)				1	1
<i>Paramerina parva</i> (Freeman 1961)	1		1	1	3
<i>Tanytarsus</i> sp. 1				1	1
Coleoptera				1	1
<i>Antiporus</i> sp. 1					
<i>Dryopidea</i> sp. 1		1	1		2
<i>Hydrochus</i> sp. 1		1			1
Hydrophilidae				1	1
<i>Hyphydrus elegans</i> (Montrouzier 1860)		1		1	2
<i>Limnodessus</i> sp. 1	1	1	1	1	4
Hemiptera	1				1
<i>Sigara (Tropocorixa) mullaka</i> Lansbury 1970					
Gerridae sp. 1			1		1
Hebridae sp. 1		1			1
Vellidae sp. 1		1			1
Odonata					
<i>Austrolestes io</i> (Selys 1862)			1		1
<i>Austroagrion coeruleum</i> (Tillyard 1908)		1	1		1
<i>Austrogomphus</i> sp. 1			1		1
<i>Austrolestes analis</i> (Rambur 1842)			1		1
Trichoptera					
Leptoceridae sp. 1	1	1	1	1	4
Leptoceridae sp. 2		1	1		2
ACARINA					
Hydracarina					
Pionidae sp 1		1		1	2
Pionidae sp. 2				1	1
Oribatida spp				1	1
OLIGOCHAETA: Naididae					
<i>Pristinella jenkiniae</i> (Stephenson 1931)		1	1		2
NEMATODA spp	1	1	1		3
TOTAL	14	23	24	18	

DISCUSSION

In terms of ionic dominance and equivalent proportions, the ionic pattern of EPP 173 is typical of many surface waters on the Swan Coastal Plain (Williams 1967), indicative of both the seawater origin of the water and of little geochemical modification, consistent with movement of groundwater through chemically unreactive siliceous Bassendean sands underlying the wetland. Indeed, in terms of the ionic pattern and conductivity and pH values, the water properties of EPP 173 were similar to those of the southern wetlands containing *G. nigrostriata* populations (Smith 1996). The most notable and unusual feature of EPP 173 is its very dark water colour during spring and summer which provides the conditions for the development of a pronounced temperature stratification of the water column. Davis and Rosich (1993) suggested that water of Swan Coastal Plain swamps with colour values ≥ 352 $\text{g}_{440} \text{m}^{-1}$ or 300 HU should be classified as coloured. Conversion of the TCU (\equiv Gilvin) values for EPP 173 swamp gives an HU value >6900 [following the conversion of Kirk (1983: p.56) cited by Schmidt and Rosich (1993: p.42)], considerably higher than the maximum HU values <600 for Swan Coastal wetlands cited by Schmidt and Rosich (1993) including the seven dark water swamps about Perth in the Gowns *et al.* (1993) study.

This temperature stratification, resulting from the interaction between solar heating and light attenuation in highly coloured water, is crucial for the retention of the minnow in EPP 173 (Smith *et al.* 2002a). Ryder and Horwitz (1995) observed transient temperature gradients of up to 6.6°C in Lake Jandabup despite the lake being only slightly coloured (2 to $17 \text{g}_{440} \text{m}^{-1}$) (Sommer and Horwitz, 1999). They suggested that the establishment of temperature gradients could be a feature of all dark-water lakes on the Swan Coastal Plain. In order to maintain the population of *G. nigrostriata* in EPP 173, the temperature stratification must be reliable and stable against wind mixing during the daytime; due to cool overnight temperatures the stratification is unlikely to persist through the night. To mix an open lake the size of EPP 173 would require prevailing winds of 5 ms^{-1} for 14 hrs, 7.5 ms^{-1} for 5 hrs, or 10 ms^{-1} for 2 hrs (pers. comm., Dr D Horn). Some wind data are available from nearby weather stations at Perth airport and Pearce airbase, however these do not report wind speed continuously and cannot be compared to these thresholds. Winds exceeding 21 kmh^{-1} (5 ms^{-1}) are common at both stations but are unlikely to blow at this velocity for periods anywhere near 14 hours; the southwesterly sea-breeze, a dominant feature of the climate of southwestern Australia, is an afternoon phenomenon of not >6 hours duration. We do not see wind mixing as an immediate threat

to the thermal stratification and subsequently to the *G. nigrostriata* population in EPP 173; however, the emergent and surrounding vegetation need to be maintained.

EPP 173 is a wetland of major conservation significance, harbouring a population of *G. nigrostriata* some 350 km north of the main area of distribution of the species. In terms of invertebrate fauna it has an unusually high (22%) proportion, of benthic cladocerans which compares to $\approx 14\%$ for other Swan Coastal Plain wetlands reported on by Gowns *et al.* (1993). One of the EPP 173 cladoceran species (*Rak obtusus*) also represents a northern outlier population with a similar distribution to *G. nigrostriata*. Another chydorid cladoceran from this wetland could not be keyed out, even to genus, and is likely to be a new species. This rich benthic cladoceran fauna, a major component of the diet of the resident Black-stripe minnow, (Smith 1996) possibly contributed to the persistence of this northern population. The total of 41 species is within the range (34–61) of species recorded from the seven dark-water swamps in the Gowns *et al.* (1993) study of 40 lakes on the Swan Coastal Plain near Perth. EPP 173 was somewhat unusual, compared to other Swan Coastal Plain wetlands, in that it contained no molluscs and only a single ostracod species – this is most likely a reflection of the low CaCO_3 concentrations of this wetland. The remaining fauna of EPP 173 was similar to that of other wetlands of the Swan Coastal Plain (Gowns *et al.* 1993). Further, unlike many other wetlands of the Swan Coastal Plain, EPP 173 is still in a relatively pristine condition with no exotic fauna, low nutrient levels and an absence of algal blooms. The very low abundance of microalgae was especially well illustrated by the very low chlorophyll and phaeophytin concentrations measured in the present study.

Given the importance of the special eco-physiological conditions operating in EPP 173, how likely is the wetland to continue operating with its present limnological pattern in the face of increasing urbanisation along the North East Corridor? Details of the hydrological cycle are unknown, even of the relative contributions from rainfall directly and groundwater. However, the shift to much more intense land use and increasing urbanisation generally through the area will inevitably mean greater: human intrusion, environmental degradation, fire frequency and destructiveness than is occurring now. Consequently, the hydrological cycles driving the limnology of EPP 173 will undoubtedly alter, increasing the probability for extinction of the resident population of *G. nigrostriata*. Tumulus springs, also dependent on groundwater discharge and once common along nearby Ellen Brook valley, are reduced to three structures; their importance

stems from their provision of a specialised micro-environment which harboured northern outlier populations of moisture-dependent animals and plants within the xeric climate of the mid-Swan Coastal Plain (Knott and Jasinska 1998).

ACKNOWLEDGEMENTS

We sincerely acknowledge help from: Sharon Stratico and Jeff Kite, Water and Rivers Commission, Perth; and from David Horn, Centre for Water Research, The University of Western Australia, for kindly calculating the wind velocities required to mix EPP 173 on warm summer days. Funding from Rivers and Waters Commission, and the Department of Zoology, The University of Western Australia, is also acknowledged.

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Very old patelliform gastropods from the Early Cambrian of China: Reconsideration of the systematic position of *Archaeotremaria*

Yu Wen

Nanjing Institute of Geology & Palaeontology, Chinese Academy of Sciences,
Nanjing, 210008, People's Republic of China

Present address: Department of Earth & Planetary Sciences, Western Australian Museum,
Francis Street, Perth, Western Australia, 6000, Australia. Email: wenyu@hotmail.com

Abstract – *Archaeotremaria polytremata* Yu from the Lower Cambrian Maidiping Member of the Hongchunping Formation of Sichuan, China, was originally described as a primitive monoplacophoran. A restudy of the holotype and paratype has led to a reconsideration of its systematic position. *A. polytremata* has a patelliform shell with a series of median-dorsal tremata extending from the apex to the anterior margin and periodic rugae. The species is now reassigned to the Gastropoda, rather than Monoplacophora.

INTRODUCTION

The fossils redescribed and refigured in the present paper were collected by the writer and his colleagues in 1977 from the upper part of the Lower Cambrian Maidiping Member of the Hongchunping Formation. The section is situated at the west side of Gaoqiao village, about 14 km south of the city of Emei, Sichuan, China. The Maidiping Member is about 32 m in thickness; it is composed mainly of light to dark inequigranular arenaceous dolomites with collophane. The member conformably overlies the Precambrian Maoergang Member of the Hongchunping Formation and is overlain conformably by the Lower Cambrian Jiulaodong Formation (Yin *et al.* 1980) (Figure 1). The Maidiping Member is one of several units in the Yangtze region of China which are rich in micro-molluscan fossils. Specimens of *Archaeotremaria polytremata*, often occur together with interesting and characteristic forms of the Meishucun Stage, such as *Watsonella yunnanensis* (He and Yang), *Circotheca subcurvata* Yu, *Merismoconcha multisegmentata* Yu, *Maidipingoconus maidipingensis* (Yu) and *Yangtzeconus priscus* Yu. These fossils are widely distributed in eastern Yunnan, western Hubei and southwestern Shaanxi.

The patelliform fossil *Archaeotremaria polytremata* Yu, was described by the writer in 1979 as a member of the Class Monoplacophora. A restudy of the holotype and paratype has concentrated on some characters which previously were uncertain, such as the concentric periodic rugae, and a development of tremata throughout ontogeny. These observations provide the basis for reconsidering the systematic position of the genus.

Illustrated specimens are housed in the Nanjing Institute of Geology and Palaeontology, Chinese

Academy of Sciences, Nanjing, People's Republic of China.

SYSTEMATIC PALAEONTOLOGY

Class Gastropoda Cuvier, 1797

Subclass Prosobranchia Milne-Edwards, 1848

Order Archaeogastropoda Thiele, 1925

Suborder Bellerophonitida Ulrich and Scofield,
1897

Superfamily Archaeotremarioidea Yu, 1979

Family Archaeotremariidae Yu, 1979
(= Granoconidae Yu, 1979)

Diagnosis

Shell minute to small, univalve, bilaterally symmetrical, patelliform, cyrtconic; with a series of tremata on the median dorsal side.

Remarks

The family Granoconidae Yu was established by the writer in 1979 p. 265, based on the genus *Granoconus* Yu, 1979. Subsequent detailed comparison demonstrated that *Granoconus* is quite similar to *Archaeotremaria* Yu, 1979: 249, especially in the dorsal tremata on tubular projections. For this reason, the genus *Granoconus* was relocated in the family Archaeotremariidae Yu, 1979 by the writer in 1987. It follows therefore that the family Granoconidae should be considered a junior synonym of the family Archaeotremariidae (Yu, 1987b: 170).

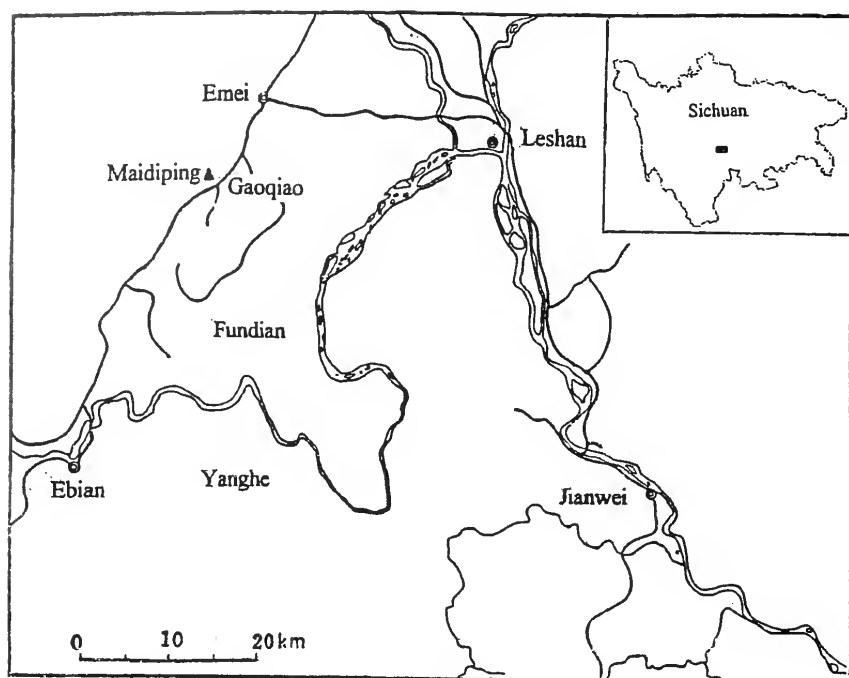


Figure 1 Sketch map showing the fossil locality.

This family was erected to include three genera: *Archaeotremaria* Yu, 1979 from the Lower Cambrian Maidiping Member of Hongchunping Formation in western Sichuan, *Granoconus* Yu, 1979 from the Lower Cambrian Huangshandong Member of Tongying Formation in western Hubei, China and *Rozanoviella* Missarzhevsky, 1981 from the Lower Cambrian Tommotian to Atdabanian Stages of western Mongolia.

Genus *Archaeotremaria* Yu, 1979 emend.

Archaeotremaria Yu, 1979: 249, 264; Dzik, 1981: 119; Yu, 1983: 1572; 1987a: 55; 1987b: 170; 1990: 144; 1996: 211.

Type species

Archaeotremaria polytremata Yu, 1979: 249, 264, by original designation, from Lower Cambrian Maidiping Member of Hongchunping Formation, at Maidiping of Emei, Sichuan, China.

Diagnosis

Minute, patelliform, bilaterally symmetrical. Protoconch unknown. Apex obtusely rounded. Dorsum broadly rounded with an obtuse dorsal ridge in the central part, a series of tremata on the tubular projections on the median dorsal ridge, the tremata divided into two small pores, which were

gradually filled with shell secretion during growth, the last one remaining open and serving as an exhalant function. Aperture large, expanded, subelliptical in form. Surface ornamented with concentric, periodic rugae, growth lines and pustules. Muscle scars unknown.

Remarks

In the presence of the tremata on the tubular projections on the median dorsal ridge and ornamentation of numerous small pustules, this genus resembles *Granoconus* Yu, 1979 from the Lower Cambrian Huangshandong Member of Tongying Formation of the Hujintan section of Yichang, Hubei (Yu, 1979: 250, 265; 1987b: 173; 1990: 145). However, *Granoconus* has a cyrtconic shell, a comparatively narrow dorsal ridge and the tremata is a single pore.

The general form of the shell and the presence of a series of tremata in the central part of the dorsum, suggests comparison with *Rozanoviella* Missarzhevsky, 1981 from the Lower Cambrian Tommotian to Atdabanian Stages of western Mongolia (Missarzhevsky, 1981: 27; Zhegallo, in Voronin *et al.* 1982: 46; Zhegallo in Esakova and Zhegallo, 1996: 164), but in *Archaeotremaria* the shell has larger and fewer tremata on the tubular projections, of which the last remains open. In *Rozanoviella*, the numerous small tremata on the median dorsal ridge are chain-like in appearance;

in *Archaeotremaria*, the tremata are divided into two small pores, whereas in *Rozanoviella* the trema is a single pore.

In *Archaeotremaria*, the presence of a series of median dorsal tremata is similar to the condition in the bellerophonitoidean gastropods *Tremanotus* Hall, 1865, both sharing such common features as: 1) bilaterally symmetrical shell, 2) the possession of a series of median dorsal tremata on the tubular projections, 3) the periodic rugae, and 4) an expanded aperture. However, there are still great differences between them, particularly in the shell being patelliform in *Archaeotremaria*, while the isostrophic form characterises *Tremanotus*. In *Archaeotremaria*, the tremata are divided into two small pores, whereas in *Tremanotus*, the tremata are a single pore. In the former, the apex is situated at the posterior part of the shell, but in the latter, the earliest whorl is succeeded by the later closely coiled ones.

In the general aspect of the tremata on tubular projections, *Archaeotremaria* somewhat resembles *Knightites* Moore, 1941 from Upper Pennsylvanian of Kansas. However, *Knightites* has an isotrophic shell, spiral ornament and projecting tubes on either side of the selenizone.

Archaeotremaria polytremata Yu

Figures 2 A–I; 3 A–D

Archaeotremaria polytremata Yu, 1979: 249, plate 4, figures 6–11, text-figure 6; 1987a: 55, plate 3 figures 3, 4; 1987b: 171, plate 33, figures 1–5; plate 34, figures 1–5, text-figures 21, 52; 1990: 162, plate 7, figures 1–3; 1993: 241, text-figure 23.

Material Examined

Holotype

NIGP 54460, in the collections of the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences. Collected by the writer in 1977 from the Lower Cambrian Maidiping Member of Hongchunping Formation at Maidiping of Emei, Sichuan, China.

Paratype

NIGP 54461 from same locality and horizon as the holotype.

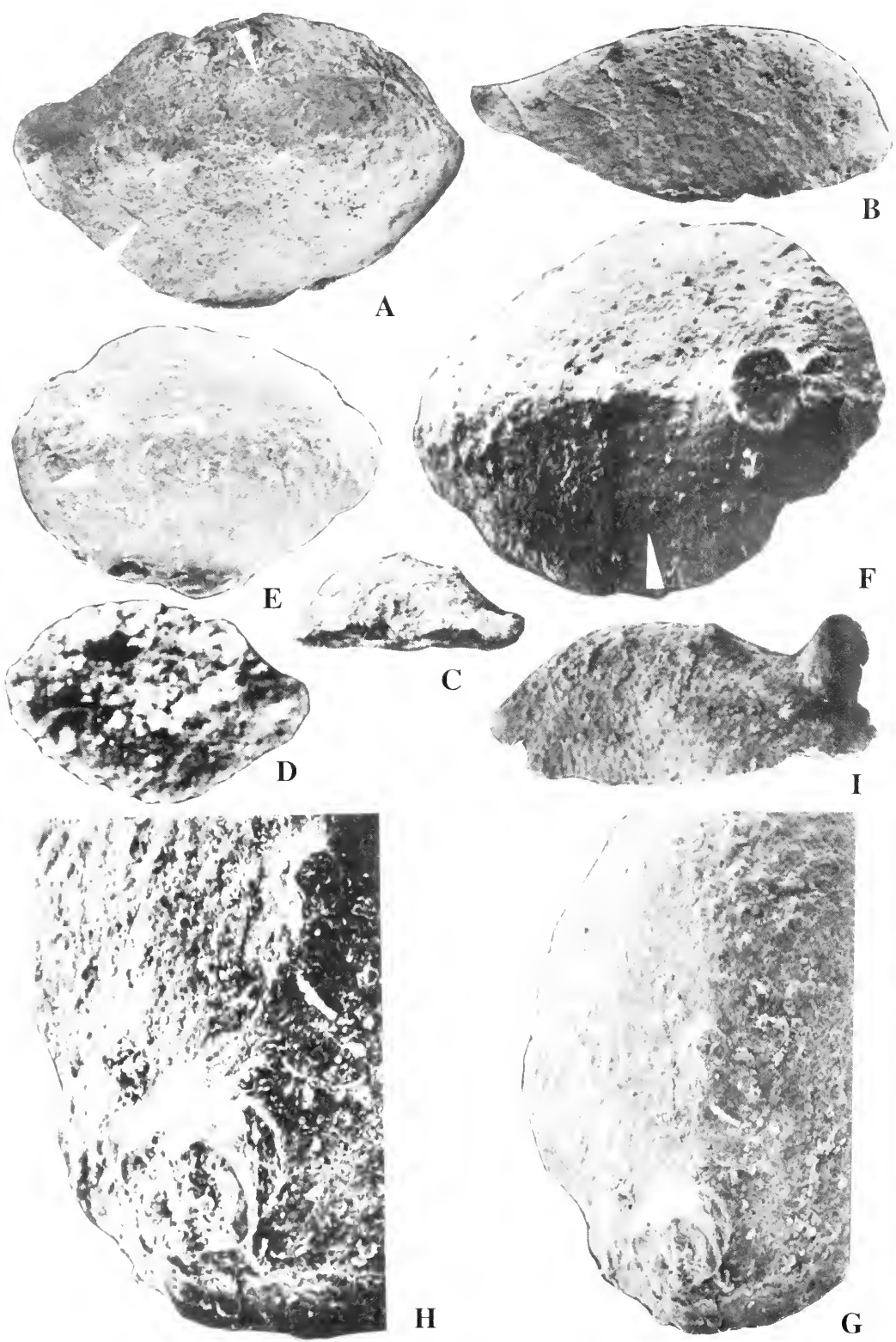
Description

Minute, patelliform, bilaterally symmetrical. Protoconch unknown. Apex bluntly rounded, slightly in posterior part of centre. Subapical area scarcely rounded and inclined to the posterior margin. Lateral slopes broadly rounded. Dorsal side broadly rounded, moderately convex, gradually sloping to the anterior margin, with an obtuse dorsal ridge in the central part of the dorsum, and a

series of tremata on the median dorsal ridge. The earliest tremata unclear, about seven tremata can be observed on the mould, usually on the tubular projections. First trema very small and moderately protruding, closed by shell secretion, situated about one-third of the posterior margin from the shell. Second and third tremata small, subcircular, a little protruding and closed by shell secretion. The fourth trema strongly protruding, inclined forward, broadly rounded in the basal part, gradually tapering toward the top, situated at about one-third of the anterior margin from the shell, just on the periodic ruga and also closed. The fifth trema slightly protruding, poral margin slightly broken, but the general form and periodic ruga can be seen. The poral wall of the sixth trema broken, remaining a subcircular pore. Pore small, situated between the middle part of the two periodic rugae. The last one is the highest and biggest one in the series of tremata, subelliptical in plan view. Poral wall thickened, upper part of poral wall a little convexly arched first, then gradually, concavely inclined and extending downward, forming a V-shaped septum, dividing the trema into two small pores; pore subreniform in outline and equal in size, located near the anterior margin, and serving as an exhalant function.

Surface ornamentation of the shell is not preserved, although some regularly distributed periodic rugae are still visible on the apical area, and sub-apical area, especially the latter, where at least five periodic growth rugae can be seen on the anterior part of the dorsum (Fig. 3A). The inner periodic growth ruga is complete, forming a ring on the dorsum, situated behind the second trema. The second and third periodic growth rugae are similar morphologically to the inner one, located behind the third and fourth tremata. The fourth and fifth periodic growth rugae are not well preserved due to the periphery of the shell being slightly broken. Aperture large, occupying most of the ventral side, subelliptical in shape, posterior margin narrowly rounded, lateral sides broadly arcuated, anterior margin not known in detail.

The paratype, shown in Figures 2E–I, 3C–D, is a well preserved internal mould. It is very small, possibly a juvenile. In plan view, the shell is elliptical in shape. Dorsal side strongly arched, broadly rounded, gradually sloping to anterior margin. Posterior margin narrowly rounded, lateral slopes gently arcuated. The centre of the shell has an obtuse dorsal ridge, with four tremata on tubular projections. First two tremata very small, scarcely projecting, located near the apical area. Third trema distinctly protruding and inclined forward, broadly rounded in the basal part, slowly constricted to the top; poral wall thin and subelliptical in shape, narrowly rounded posteriorly, broadly curved laterally, narrow anteriorly, divided into two small



pores by a thin septum and closed by shell secretion. The last tremata is the largest and highest, strongly protruding and slightly inclined forward; poral opening circular in plane view, slightly flared and reflected, the anterior part seems to extend a little forward (Figure 2F); nearly heart-shaped in anterior view (Figures 2F–H, 3D). Posterior surface of poral wall is thickened, and a little swollen. Lateral parts slightly convex initially, middle part flatly concave, gradually sloping and extending downward, forming a "V" shaped septum dividing the opening trema into two small pores, which are equal in size and reinform in outline.

Surface ornamented with numerous small pustules, among which can be observed several rows of pustules that seem to correspond to periodic growth rugae. Muscle scars unknown.

Dimensions (mm)

	Length	Height	Width
NIGP 54460	1.500	0.546	1.000
NIGP 54461	0.588	0.210	0.448

Horizon and locality

Maidiping Member of Hongchunping Formation at Maidiping of Gaoqiao, Emei.

Discussion

In 1979, the writer established the family Archaeotremariidae Yu, 1979 within the Class Monoplacophora based on the genus *Archaeotremaria* Yu, 1979. In addition to the type genus, Yu (1987b) assigned *Granoconus* Yu, 1979 from the Lower Cambrian Huangshandong Member of the Tongying Formation of Yichang, Hubei, China and *Rozanoviella* Missarzhevsky, 1981 from the Lower Cambrian Tommotian to Atdabanian Stages of western Mongolia to this family. Nevertheless, he pointed out that *Archaeotremaria* possessed a row of tremata on the tubular projections on the dorsal ridge that differed from the all known genera in the Monoplacophora (Yu, 1979: 249). The term Class Monoplacophora was abandoned by Peel (1991), who proposed using the Class Tergomya, Horny 1965, for forms possessing a bilaterally symmetrical exogastric shell with bilaterally symmetrical muscle scars (Peel, 1991a; Berg-Madsen and Peel, 1994; Yochelson, 1994; Horny'

and Peel, 1996; Webers and Yochelson, 1999; Yu and Yochelson, 1999).

The species *Archaeotremaria polytremata* is very small. The very small size (about 1–2 mm) of the Early Cambrian molluscs has been discussed in detail by many scholars (Runnegar and Jell, 1976; Runnegar and Pojeta, 1985; Chaffee and Lindberg 1986; Salvini-Plawen, 1990; Dzik, 1991; Peel, 1991; Haszprunar, 1992). The holotype of *A. polytremata* is 1.500 mm in length, with seven tremata on the dorsal ridge. The paratype is a juvenile 0.588 mm long, with four tremata.

The molluscan character of this species taxon is shown the following combination of characters: bilaterally symmetrical, patelliform shape, with apex located slightly posterior of centre; aperture ventral; dorsal side broadly rounded, the tremata series marked by tubular projections along the median dorsal ridge, which were infilled sequentially with shell growth. The last of these remained open, serving the exhalant function. At least five periodic growth-rugae can be seen on the dorsal side of the internal mould.

Among the Early Paleozoic molluscan fauna, there are a few genera of bellerophontoidean gastropods which have one or more tremata on the median dorsal side, such as the Lower Cambrian *Granoconus trematus* Yu, 1979 (Yu, 1979, plate III, figures 33–35, text-figure 7; 1987b, plate 33, figures 6–9, text-figure 53; Figure 3E–3F), *Rozanoviella atypica* Missarzhevsky, 1981 (Missarzhevsky 1981, plate III, figure 9, text-figure 2; Zhegallo in Voronin *et al.*, 1982, plate I, figures 10–11; Zhegallo in Esakova and Zhegallo 1996, plate XX, figures 4–5; Figure 3G–3I); the Middle Ordovician-Silurian *Tremanotus* Hall, 1865, (Lindström, 1884; Knight, 1941; Knight *et al.*, 1960; Horny', 1963; Yochelson, 1967; Peel, 1972, 1991b) and *Salpingostoma* Roemer, 1876 (Lindström, 1884; Knight, 1941, 1952; Knight *et al.*, 1960; Peel, 1991b). Nevertheless, so far as I am aware, no monoplacophoran or tergomyan has dorsal tremata.

It is worth noting that *A. polytremata*, not only has a series of tremata on tubular projections from the apex to the anterior margin on the median dorsal side, but there also seems to be a periodicity in its formation. With the growth of the shell, the previously formed trema is gradually filled with shelly substance and then subsequently a new trema develops, remaining open and serving as an exhalant outlet. It can be demonstrated that the tremata develop throughout

◀ **Figure 2** A–I, *Archaeotremaria polytremata* Yu. A–D, holotype NIGP 54460. A, dorsal view, showing seven tremata on the median dorsal ridge from the apex to anterior margin and some concentric, periodic growth rugae (arrow), x 55. B, left lateral view, x 50. C, right lateral view, x 36. D, apertural view, x 40. E–I, paratype NIGP 54461. E, oblique dorsal view, showing four tremata on tubular projections on the median dorsal ridge and some traces of concentric, periodic growth rugae (arrow), x 120. F, dorsal view, showing the tremata and sculpture, x 180. G–H, enlargement of the last two tremata and sculpture, showing the tremata are divided into two small pores by a V-shaped septum, x 200 and x 300. I, right lateral view, showing four narrow bands, x 120.

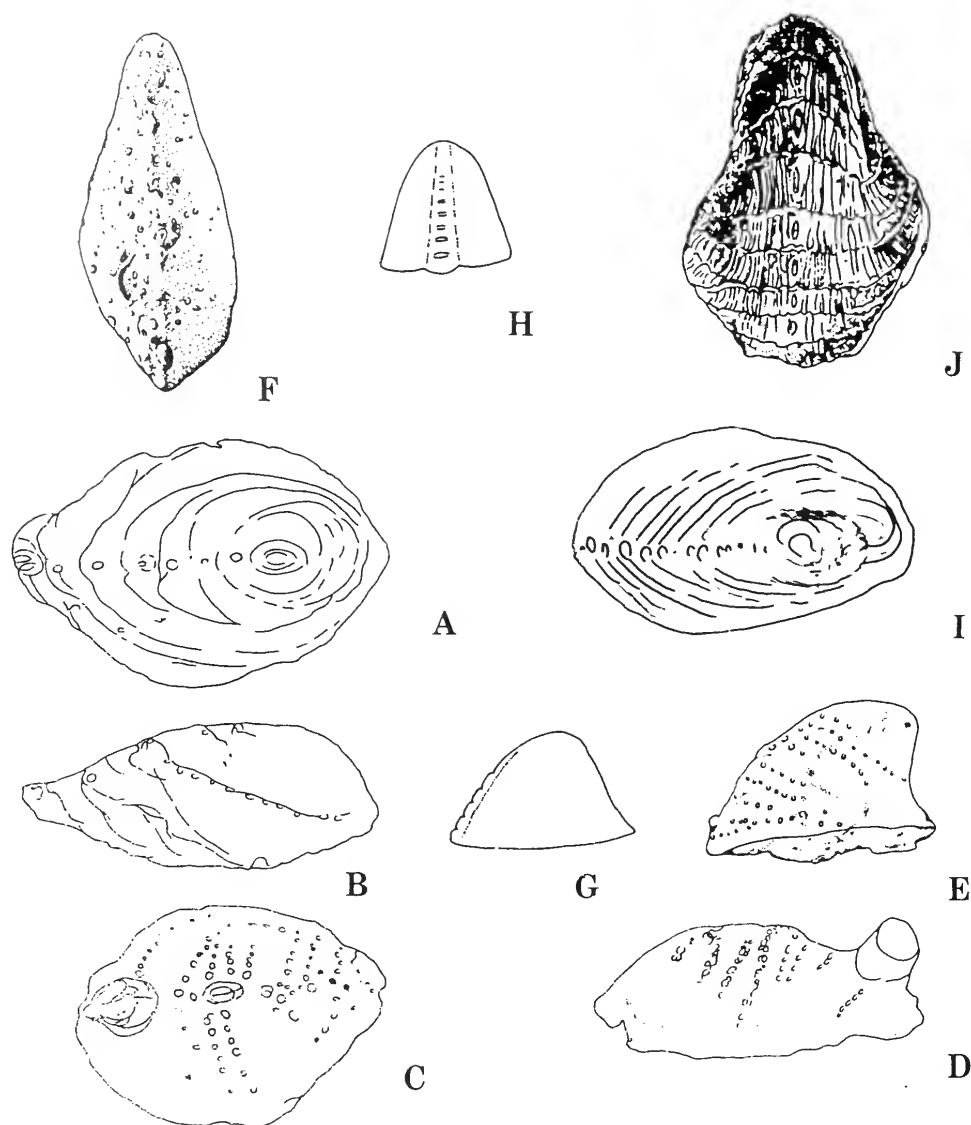


Figure 3 A–D, *Archaeotremaria polytremata* Yu. A–B, holotype NIGP 54460. A, dorsal view, showing tremata and concentric, periodic growth rugae, $\times 38.5$. B, left lateral view, showing tremata on the tubular projections, $\times 35$. C–D, paratype NIGP 54461. C, dorsal view, showing the tremata and some pustules, $\times 85$. D, right lateral view, showing four narrow bands, $\times 85$. E–F, *Granoconus trematus* Yu, holotype NIGP 54455. E, left lateral view, showing tremata on the tubular projections $\times 32$. F, anterior view, $\times 42$. Lower Cambrian of Hubei, China (after Yu Wen, 1979). G–I, *Rozanoviella atypica* Missarzhevsky, G, left lateral view, $\times 30$. H, anterior view, $\times 30$. Lower Cambrian of western Mongolia. (after Missarzhevsky, 1981). I, dorsal view, $\times 55$. Lower Cambrian of western Mongolia (after Zhegallo in Voronin *et al.*, 1982). J, *Trematodus longitudinalis* Lindström. dorsal view, $\times 1$. Middle Silurian of Gotland, Sweden, (after Lindström, 1884).

ontogeny in *Archaeotremaria*. The tremata of *A. polytremata* are divided into two small pores, indicating that *Archaeotremaria* may be a gastropod having paired tentacles. However, the living monoplacophoran *Neopilina galathea* Lemche (1957, figures 1–4) and *Vema ewingi* Clarke and Menzies

(1959, figures 1–2) have five and six pairs of gills respectively. *Pilina liaoningensis* Yu and Yochelson (1999, figures 2a, 2b, 3f, 3g, 4a, 4b) from the Upper Cambrian Wanwankou Member of Fengshan Formation of Liaoning, China has five pairs of scars of the gill cavity.

The form of the tremata and their presumed function in *Archaeotremaria* are very similar to those of the Middle Ordovician *Trematodus* Hall, 1965. Though distant from each other in absolute geologic time, such gaps within plausible or speculative lineages are not unusual in view of our far from complete knowledge of Early Paleozoic molluscs. Ongoing new discoveries and research can be expected to close some of the gaps separating Early Cambrian and Middle Ordovician trematose molluscs. It has long been argued that bellerophontids are most similar to pleurotomarians (Meek, 1866; Lindström, 1884; Ulrich and Scofield, 1897). During the last fifty years, there have been many contributions concerning similarities between bellerophontoidean gastropods and pleurotomarians (Knight, 1947, 1952; Knight *et al.* 1960; Yochelson, 1967, 1984; Peel, 1972, 1991b; Batten, 1975; Golikov and Starobogatov, 1975; Linsley, 1978; McLean, 1984). The appearance of the primitive patelliform *Archaeotremaria* in the Early Cambrian, may provide some evidence for further discussion on the relationship between the bellerophontoidean gastropods and the pleurotomarians. Moreover, the presence of regularly distributed periodic rugae is another noteworthy feature in this genus; at least five concentric, periodic growth rugae can be seen on the internal mould, periodically spaced, usually between the tremata. This character is similar to that of *Trematodus portlocki* Reed (1920–1921, plate XIII, figure 4) from the Ordovician of Tyrone, United Kingdom, *Trematodus longitudinalis* Lindström (1884, plate III, figures 39–40; plate IV, figures 5, 6; Figure 3J) from the Lower Silurian of Gotland, Sweden and of *Trematodus tuboides* Perner (1903, plate 82, figures 11–15, text-figure 88; Horny', 1963, plate XVIII, figures 1–5) from the Middle Silurian Wenlockian Stage of Central Bohemia. Therefore, *Archaeotremaria* is quite different from tergomyans, but closely resembles certain gastropods.

Furthermore, the most important distinguishing feature of *Archaeotremaria* is that the surface of the internal mould bears numerous small pustules, especially on the right side of the paratype (NIGP 54461), where there are four narrow bands, from the median dorsal side, extending slightly backward. Previously Yu regarded these narrow bands as muscle scars in the inner surface (Yu, 1987a, plate 3, figures 3–4; 1987b, plate 34, figures 1–5, Text figure 52; 1990, plate 7, figures 1–3; 1993, Text-figure 23). After re-examination of the holotype and the paratype of the type species, I consider that four pairs of muscle scars do not exist. The interior of the shell in the Class Tergomya is characterised by bilaterally symmetrical muscle scars on the bilaterally symmetrical shell.

In summary, it has been shown that *Archaeotremaria* has a patelliform shell with a series

of median dorsal tremata and periodic growth rugae. This combination of characters clearly indicate that *Archaeotremaria polytremata* is a primitive patelliform gastropod rather than Tergomya.

ACKNOWLEDGEMENTS

I would like to take this opportunity to thank K.J. McNamara and G.W. Kendrick, Western Australian Museum and two anonymous reviewers. Thanks also to Danielle West and Anne Nevin for their technical assistance.

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Guide to Authors

Subject Matter:

Reviews, observations and results of research into all branches of natural science and human studies will be considered for publication. However, emphasis is placed on studies pertaining to Western Australia. Longer papers will be considered for publication as a Supplement to the *Records of the Western Australian Museum*. Short communications should not normally exceed three typed pages and this category of paper is intended to accommodate observations, results or new records of *significance*, that otherwise might not get into the literature, or for which there is a particular urgency for publication. All material must be original and not have been published elsewhere.

Presentation:

Authors are advised to follow the layout and style in the most recent issue of the *Records of the Western Australian Museum* including headings, tables, illustrations and references.

The title should be concise, informative and contain key words necessary for retrieval by modern searching techniques. An abridged title (not exceeding 50 letter spaces) should be included for use as a running head.

An abstract must be given in full length papers but not short communications, summarizing the scope of the work and principal findings. It should normally not exceed 2% of the paper and should be suitable for reprinting in reference periodicals.

The International System of units should be used.

Numbers should be spelled out from one to nine in descriptive text; figures used for 10 or more. For associated groups, figures should be used consistently, e.g. 5 to 10, not five to 10.

Spelling should follow the *Concise Oxford Dictionary*.

Systematic papers must conform with the International Codes of Botanical and Zoological Nomenclature and, as far as possible, with their recommendations.

Synonymies should be given in the short form (taxon, author, date, page) and the full reference cited at the end of the paper. All citations, including those associated with scientific names, must be included in the references.

Manuscripts:

The original and two copies of manuscripts and figures should be submitted to the Editors, c/- Publications Department, Western Australian Museum, Francis Street, Perth, Western Australia 6000. They must be in double-spaced typescript on A4 sheets. All margins should be at least 30 mm wide. Tables plus heading and legends to illustrations should be typed on separate pages. The desired position for insertion of tables and illustrations in the text should be indicated in pencil. Tables should be numbered consecutively, have headings which make them understandable without reference to the text, and be referred to in the text.

High quality illustrations are required to size (16.8 cm x 25.2 cm) or no larger than 32 cm x 40 cm with sans serif lettering suitable for reduction to size. Photographs must be good quality black and white prints, not exceeding 16.8 cm x 25.2 cm. Scale must be indicated on illustrations. All maps, line drawings, photographs and graphs, should be numbered in sequence and referred to as Figure/s in the text and captions. Each must have a brief, fully explanatory caption. On acceptance a computer disk containing all corrections should be sent with amended manuscript. The disk should be marked with program (e.g. Word, WordPerfect, etc).

In papers dealing with historical subjects references may be cited as footnotes. In all other papers references must be cited in the text by author and date and all must be listed alphabetically at the end of the paper. The names of journals are to be given in full.

Processing:

Papers and short communications are reviewed by at least two referees and acceptance or rejection is then decided by the editors.

The senior author is sent one set of page proofs which must be returned promptly.

The senior author will receive fifty free offprints of the paper. Additional offprints can be ordered at page proof stage.

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